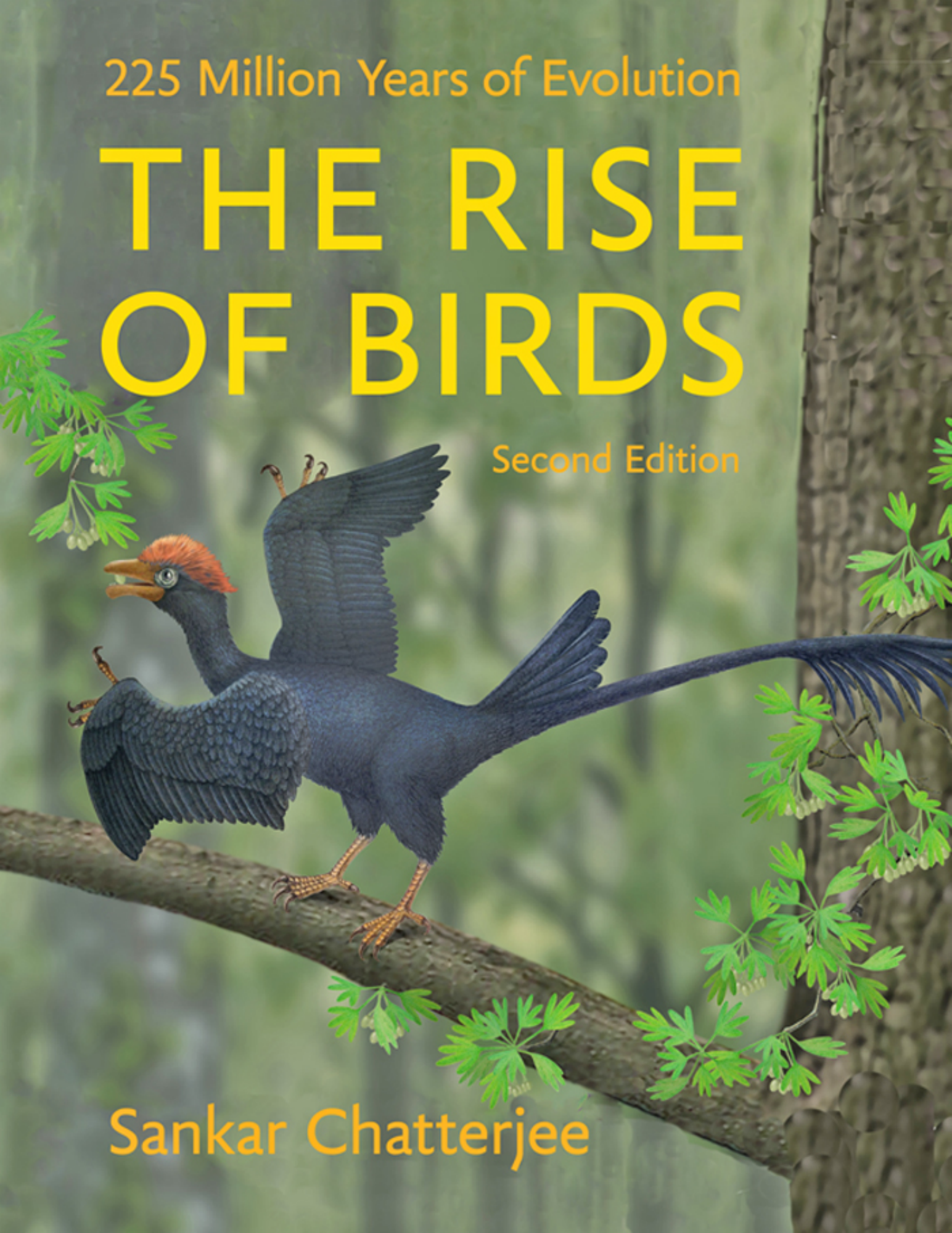
225 Million Years of Evolution

THE RISE OF BIRDS

Second Edition



Sankar Chatterjee

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The Rise of Birds

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225 Million Years of Evolution

Second Edition

Sankar Chatterjee

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For Sibani, with my love

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Preface to the Second Edition

Endowed with colorful plumages and beautiful songs, birds in flight symbolize spirits released from the bondage of gravity. From the day that humans first looked up at the skies, birds have summoned a sense of wonder and mystery, enchanting our earthbound ancestors with their freedom and song. They fly where they please and when they please. The power of flight has opened up to birds a multilayered network of aerial highways and byways, enabling them to reach any place on our planet. They exhibit a wide variety of sizes, shapes, colors, and habits. Their awesome power of flight takes them to every continent, from pole to pole, and they fill every conceivable niche. Birds have enriched our life with their free spirit, beauty, and songs. They inform us about the rest of the natural world, control insect population, disperse seeds, and embody key values in human cultures. They have played a key role in many important developments of evolutionary theories. Given their stark beauty, graceful flight, exuberant activity, diurnal habits, dazzling feathers, and melodious songs, it is hardly surprising that birds feature strongly in every culture in painting, poetry, and music. Birds are the most successful terrestrial vertebrate, abundant in both numbers of species and populations. About 300 billion birds, with 10,000 species, now inhabit the Earth, as compared to 3,000 species of amphibians, 6,000 species of reptiles, and perhaps 4,500 species of mammals.

Birds are one of the oldest, most successful, and fascinating groups of flying vertebrates in our landscape. The story of bird evolution as revealed by the study of fossils is important not only to paleontologists but also to those engaged in other branches of science—geology, biology, ecology, evolution, and natural history—as well as the general public. Although living birds are one of the best-known groups of extant vertebrates, their origin, evolution, and early adaptive radiation are poorly documented in the fossil record. Until recently, most knowledge of the early history of birds and the evolution of their flight was based on handful of diverse Mesozoic taxa widely separated in time and restricted to marine environments. The rarity of bird fossils is generally attributed to the extreme fragility, lightness, pneumaticity, arboreal habits, and general smallness of their bones. However, there is a renaissance in the study of Mesozoic birds with the spectacular discoveries of amazing fossils from China during the past two decades. These new discoveries fill major gaps in the evolutionary history of birds and provide critical insights into the origin of feathers, evolution of flight, and their phylogenetic relationships.

The Mesozoic has often been referred to as the "Dark Ages of Birds" because only a limited number of fossils such as *Archaeopteryx* from the Late Jurassic of Germany and *Hesperornis* and *Ichthyornis* from the Late Cretaceous of Kansas filled the evolutionary gaps. *Archaeopteryx* was an icon in avian evolution, being regarded as the oldest and most primitive known bird. In recent decades the narrative of bird evolution has broadened considerably with the discovery of more fossils from around the world. Our story of bird evolution began 225 million years ago when *Protoavis* took to the air over tropical Texas forests at the very dawn of the age of dinosaurs and began to diverge in many forms and fashions. Soon after the discovery of *Protoavis*, remarkable fossils of Cretaceous birds were unearthed in China, Spain, Mongolia, Australia, Madagascar, Argentina, and Antarctica. The present edition represents a radical metamorphosis of the first edition of *The Rise of Birds*, published in 1997, amplified by the remarkable discovery of feathered dinosaurs and early

birds in China that led to dramatic breakthroughs in the origin and early evolution of birds and their flight. The discovery of a large number of new species of successive clades of Jurassic and Cretaceous birds and their immediate ancestors during the past two decades from the Tiaojishan Formation and Jehol Group of China supplies the missing evolutionary history from primitive basal birds to the forerunners of modern birds, along with their theropod ancestors. A coherent picture of the origin and early radiation of birds and their relationships began to emerge for the first time from these remarkable discoveries. The newly discovered feathered theropods from China show various transitional stages of flight—from wingless, tree-climbing coelurosaurs to parachuting, to gliding, to fully winged, actively flying birds. Some of the feathered dinosaurs had brilliant plumages that suggest that feathers might have initially evolved for sexual display and species recognition and later been co-opted for flight. A forest habitat and arboreal lifestyle might have played a critical role in the origin and early evolution of birds and their flight. Once flight was perfected, these birds may have begun to exploit other ecological niches, especially rivers, lakes, and seas, where food was abundant. They also reverted to being flightless, time and again.

This new view of the origin of birds and their flight is the centerpiece of this edition, which is based on the remarkable Chinese fossils. A modern synthesis of avian evolution is also presented using paleontology, biomechanics, and heterochrony. Both the remarkable feathered dinosaurs from China and new insights from developmental biology bring the evolutionary process alive and offer a more holistic picture of bird evolution. This book is thus in great measure a new work incorporating recent discoveries of avian fossils from different parts of the globe and their significance in the study of the origin and early evolution of birds and their flight in the framework of developmental mechanisms. The role of heterochrony in the evolution of birds is also new to this edition. Similarly, a computer simulation is used to trace the origin of flight.

To follow the various trends of bird evolution through geologic time was not an easy assignment, because so many evolutionary chapters were happening at once in the Early Cretaceous Jehol Group of China. Here I follow phylogeny as the guiding principle to tell the story of evolutionary events of birds, one by one, and of trying, somehow, to relate them to each other in the geologic time scale and paleobiogeography.

The overall picture of birds being descended from maniraptoran theropod dinosaurs is now firmly established, but the transition is often fuzzy and diffuse. Recent study suggests that *Archaeopteryx*, the most primitive and celebrated bird fossil on Earth that reigned for more than 150 years since its discovery, may not be a bird after all, but just another small feathered, bird-like theropod fluttering around during the Jurassic. The jury is still out regarding the status of *Archaeopteryx*. In this book I have treated *Archaeopteryx* as a basal bird. However, *Jeholornis* from the famous Jehol aviary of China can be a potential candidate for the status of Urvogel, the true primitive bird. Using both *Archaeopteryx* and *Jeholronis* as the basal members of avialans, I trace the origin and evolution of birds from their theropod ancestors along a cladogram through time, a genealogical tree, highlighting the anatomical changes and flight refinement in successive groups or clades, their classification and phylogenetic relationships.

Bird flight is inherently fascinating and appears to have been a fundamental factor in the early success of birds, but its origins remained murky for more than two centuries due to lack of a fossil record in the Mesozoic. With the discovery of remarkable feathered theropods and early birds in China, we have a better understanding of the origin and early evolution of avian flight and feathers. Combining both fossil evidence and aerodynamics, I offer an integrated view on the evolution of avian flight.

Other than flight, I also discuss fossil eggs and embryos of birds, the role of developmental constraints in their evolution, locomotion and footprints, and the evolutionary crisis at the end of the Cretaceous. I also include the explosive evolution of birds, their macroevolution and heterochrony, their feeding and cranial kinesis,

and their recent classification. Finally, I address the association of birds with humans during the Quaternary, and their fate in our hands with the environmental collapse.

I am a paleontologist, interested primarily in questions of biological evolution. Paleontology is fundamentally historical nature. When we look at birds, we see the shadow of dinosaurs in them, their antiquity and heritage. I wrote this book with several kinds of reader in mind: first, for anyone interested in nature and natural history who takes delight in observing birds and their acrobatic flight; second, for evolutionary biologists and others interested in the question of origins. In this book I present a readable and comprehensive narrative of the early history and radiation of birds that lived with dinosaurs for 160 million years. I also discuss the major radiation of birds after the end-Cretaceous extinction that led to the modern birds we see today. My goal in this book is to make available to a wide audience an account of our current scientific understanding of the origin and evolution birds and their flight. I have aimed this book primarily at bird lovers, both amateur and professional, interested in this subject as well as evolutionary biologists.

In the first edition of the book, I gratefully acknowledged my indebtedness to numerous individuals and institutions. I would like to add that I am grateful to my Chinese colleagues, especially Zhonghe Zhou, Xing Xu, Fucheng Zhang, Dong Zhiming, and Xiao-chun Wu, for their hospitality during my stay in China. They took me to the Liaoning fossil localities to understand the taphonomy and recurrent mass mortality events, allowed me to examine some of the spectacular feathered coelurosaurs and early birds, shared their ideas with me, and provided me with excellent photos and drawings. I feel lucky to know Xing Xu and Zhonghe Zhou, who uncovered and described the buried treasures in China and introduced them to the rest of the world. Their painstaking and brilliant work truly revolutionized Mesozoic vertebrate paleontology, especially the origin and evolution of early birds. They shared their knowledge freely with me. I acknowledge my heartfelt indebtedness to R. Jack Templin, the Canadian aeronautical engineer, for fruitful collaboration on animal flight during the past two decades that resulted in several major publications. Jack was my mentor for all these years and taught me basic aerodynamics. I thank John Talent, David Alexander, and James DeLaurier for reviewing various papers on bird flight that have been incorporated here. Larry Witmer, Luis Chiappe, and Julia Clarke were always generous to share their insights on avian evolution.

I thank my many professional colleagues who provided images of their fossils for this book. Michael W. Nickell and Patricia Koemmel carefully rendered the illustrations and made the book richer with their hard work and artistic acumen. Bill Mueller improved many illustrations, Aijuan Shi did the life restoration of *Jeholornis* on the cover, and Zhonghe Zhou, Xu Xing, and Luis Chiappe gave permission to reproduce several of their artworks. The book is the result of an ongoing and sometimes heated discussion among paleontologists in the origin of birds and their flight. The debate will continue as more and more fossils are discovered. I acknowledge all of the writers and philosophers whom I have quoted at the beginning of each chapter for their wisdom and inspiration.

Vincent Burke of Johns Hopkins University encouraged me to write the second edition of the book, waited patiently for a number of years to get back the revised manuscript, and aided me throughout the preparation of this revision with fortitude. My sincere thanks go to all of the Press's editorial staff. I want to thank Maria denBoer for her skill editing that led this book to completion.

I thank my wife, Sibani, for her love and support by relieving me of the burden of household chores and for tolerating my exile in my study to complete the book. The Museum of Texas Tech University has provided me a wonderful academic environment and financial support for my research during my tenure for three decades.

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Preface to the First Edition

In the Hindu epic *Ramayana,* we find a poignant story of resurrection. The fiery sage Gautama curses his beautiful wife, Aholya, and turns her to stone with these words: "You shall remain thus for thousands of years. Only when Rama, the son of Dasharatha, passes this way will you be restored to life." Years pass. Gautama's hermitage has long been abandoned and decays with age, choked by creepers and swallowed by rainforest. Aholya waits alone in the ruins, a stone among crumbling stones. One day, after many millennia, a very young prince Rama comes across the old ashram and sees the petrified image of Aholya, waiting. In reverence, he touches her feet. Immediately, he sees tears where there once were no eyes, flesh where there had been rock. Aholya is alive once more, free from her terrible curse.

Paleontologists have long pursued petrified bones, much like the epic hero Rama. To them fossils are million-year-old Aholyas waiting to be discovered and resurrected. They put muscle and skin on these bones, color them with human passions, and give them life. They re-create the denizens of a lost world in proper chronological and evolutionary context. This book unfolds the story of *Protoavis texensis*—"first bird, from Texas." *Protoavis* predates *Archaeopteryx* by 75 million years, pushing the emergence of birds back to the Triassic period. Being the world's oldest bird, *Protoavis* provides a new view of avian origins. When I picked up two partial skeletons of *Protoavis* out of the Triassic red beds of Texas in the summer of 1983, I did not realize that they would generate so much controversy and excitement among scientists. Soon after, avian paleontology went through its own renaissance, as more Mesozoic birds were found during a span of fifteen years than had been discovered during the entire preceding century.

Dinosaurs are so popular that we often neglect their even more fascinating relatives that are still among us. Birds, the true living dinosaurs, deserve considerable respect as successful vertebrates that have evolved, adapted, and survived over a period of 225 million years. The rise of birds in the Pangean world, their flight refinement and global diversification during the continental breakup, their decline at the end of the Cretaceous period, and their explosive radiation during the Cenozoic era are some of the greatest events in the history of vertebrates. Yet their early history is obscure and just beginning to unfold. During the seventy years since the appearance of Gerhard Heilmann's monumental work *The Origin of Birds*, substantive progress has been made in the study of bird fossils and the understanding of the theropod-bird transition. No current book deals exclusively with Mesozoic birds, which compose the first two-thirds of avian history. *The Rise of Birds* is an effort to fill this void. In this book I have attempted a readable and comprehensive account of the early history of the radiation of birds in the shadow of dinosaurs; of their anatomy, function, and evolutionary trends; of the origin of flight; of fossil eggs and embryos, feathers and footprints; of the distribution of birds in the Mesozoic period; of classification and phylogenetic relationships; and of the evolutionary crisis at the end of the Cretaceous. I have also included the explosive evolution of birds during the Tertiary period and their association with humans during the Quaternary to complete my picture of the long odyssey of birds. This book is aimed at an audience beyond the confines of the paleontological community. I give detailed accounts of specific research topics that are currently highly contested or thought provoking.

* * *

I am indebted to many colleagues for help, advice, stimulating discussions, and useful insights: Walter J. Bock, Larry D. Martin, Lawrence M. Witmer, Nicholas Hotton, Storrs L. Olson, Alan Feduccia, Erich Weber, J. M. Starck, Gerhard Mickoleit, Wolfgang Maier, Paul Bühler, D. Stephan Peters, Alick D. Walker, E. N. Kurochkin, Luis M. Chiappe, P. L. Zusi, and M. Kent Rylander. The manuscript was reviewed at various stages by Lawrence M. Witmer, James E. Barrick, and Soumya Chatterjee. I gratefully acknowledge their valuable suggestions and editorial skill. The illustrations were rendered by Michael W. Nickell, who gave precious pictorial life to my text. The majority of illustrations were drawn from the actual specimens or by redrawing and sometimes combining drawings found in the original papers describing the material. For permission to use previously published material, I am grateful to the authors and publishers concerned. I acknowledge all of the writers whom I have quoted for their wisdom and inspiration. I thank many of my graduate students for assistance in the field, especially Bryan J. Small and J. Bruce Moring, who serendipitously exposed two delicate *Protoavis* skeletons with a jackhammer. I thank R. C. Miller and Jack Kirkpatrick for allowing access to their property. I am especially grateful to John T. Montford, Donald R. Haragan, Gary Edson, Jane Winer, and Richard E. Peterson of Texas Tech University for their continued support and encouragement of my research. Over the years the research was supported by grants from the National Geographic Society, Smithsonian Institution, Texas Tech University, and University of Tübingen.

Working with the professionals of Johns Hopkins University Press has been a thoroughly enjoyable and rewarding experience. Richard T. O'Grady initiated the project; David B. Weishampel of Johns Hopkins University provided the moral and intellectual support; Robert Harington, Douglas Armato, and Ginger Berman led this book to completion. I am most grateful to Linda Forlifer for improving the style and clarity of my writing and to Julie McCarthy for careful editorial assistance. My sincere thanks to all for their patience and guidance.

The Rise of Birds

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1 Mesozoic Pompeii

The fire of Lipara, Xenophanes says, ceased once for sixteen years, and came back in the seventeenth. And he says that the lavastream from Aetna is neither of the nature of fire, nor is it continuous, but appears at intervals of many years.

Aristotle (384 BC–322 BC), *De mirabilibus auscultationibus*

Ancient Roman Life in Pompeii

On the fateful morning of August 24, AD 79, the summit of Mount Vesuvius in the Campanian region of southern Italy exploded without warning. A black river of ash, lapilli, and sulfuric acid ran from the crater of the volcano down through the city of Pompeii, leaving death and destruction in its wake. The magnificent ancient city was left buried under 4 to 6 meters of volcanic ash and debris when Mount Vesuvius unleashed its fury, engulfed the surrounding area, and instantly killed the fleeing 20,000 inhabitants of the Roman resort cities of Pompeii, Herculaneum, and Stabiae. Red-hot clouds of gas and fine ash known as pyroclastic density currents flowed down the slopes of Vesuvius, engulfing Pompeii's frescoed villas, as well as its shops, public baths, and people. "Darkness fell, not the darkness of a moonless or cloudy night, but as if the lamp had been put out in a dark room," wrote Pliny the Younger, who witnessed the cataclysm from across the Bay of Naples.

Scientists have commonly accepted that the people of Pompeii suffocated from ash and gas spewing from the volcano. However, new research by a team of Italian scientists questions this assumption and suggests that the Pompeii victims were killed instantly by lethal thermal impact, not by suffocation. The exposure to extraordinarily high temperatures, close to 250°C, from pyroclastic surges and flows killed the victims of Pompeii and surrounding areas by thermal shock. And that is how the people of Pompeii died, their remains found trapped and partly preserved within ghostly body-shaped tombs within the pyroclastic flow. The corpses were horribly burned and covered by ash to form a natural mold, frozen in position. The ruined city remained fixed in time until the Spanish military engineer Rocque Joaquin de Alcubierre discovered it in 1748. During early excavations, the void spaces of ash beds left by decomposed bodies were filled in by injecting plaster of Paris to re-create the death pose of the victims. Most of the victims held either a life-like stance or a sleep-like stance indicative of a condition known as cadaveric spasm, which is instantaneous muscular stiffening associated with violent death. The damage on the ancient bones of the victims, with micro-cracks on the sur-

face and recrystallization of the interior bone structure, indicates thermal modification at a temperature ranging from as low as 300°–250°C in Pompeii, where the bodies remained intact, to as high as 500°–600°C at Oplontis and Herculaneum, where the victims' flesh was vaporized. In the desolate silence of these once vibrant cities, life and death are captured in accurate detail in the shadow of Vesuvius.

Mesozoic Pompeii

Scientists believe that volcanic eruptions in western Liaoning Province and neighboring areas in northeastern China instantly killed rich dinosaur communities from the Middle Jurassic to Early Cretaceous era similar to the violent blast that hit the Roman city of Pompeii. Much like the residents of Pompeii, the Liaoning dinosaurs were entombed in ash and frozen in their death throes.

Rich fossil deposits representing a wide variety of life with fully articulated skeletons, often associated with soft tissues, were found in this area. Unusual and rare preservation sites of ancient life such as these are called Lagerstätten. They capture ecological "snapshots" from a moment in time when extraordinary local conditions have preserved a wide range of undisturbed fossilized organisms. The Early Cretaceous lacustrine sediments of the Jehol Group, interbedded with ash beds, comprise three geological formations—the Dabeigou, Yixian, and Jiufotang Formations, ranging in age from 130 to 120 million years ago (Zhou and Zhang 2007). In the layers of these ash beds interbedded with lake deposits, some of the most significant animals in the dinosaur world were preserved in exquisite form.

Unlike the victims of Pompeii, the famous inhabitants of Jehol—the feathered dinosaurs and their contemporaries—were buried recurrently for millions of years and sealed in time in the ash beds. The Jehol biota represents an exceptionally preserved past ecosystem of terrestrial and freshwater faunal and floral communities in unprecedented detail. Here on the shores of ancient lakes, thousands of plants, insects, fish, dinosaurs, birds, and mammals all died simultaneously—in recurrent mass mortality events that lasted for 5 million years. The discovery of the lost Jehol biota captivated the world because of its variety and beauty. Every year or two of digging uncovered more dazzling evidence of early flowering plants, or early feathered dinosaurs, or birds, or early mammals, providing a wealth of information about the ecology and environment of the Early Cretaceous Jehol biota (fig. 1.1).

The Jehol Fossils

The Jehol Group is mainly distributed in northern Hebei Province, western Liaoning Province, and southwestern Inner Mongolia, all in northeastern China. Comparable deposits of similar age occur across northern China and adjacent areas of eastern and Central Asia, including Kazakhstan, Mongolia, Siberia, Japan, and Korea, and many of these have yielded fossils very much like those of the Jehol biota (Zhou et al. 2003). However, among these fossil sites, the Liaoning Province has gained prominence as one of the best fossil sites in the world. The lithology of the Jehol Group comprises layers of basalts interbedded with lacustrine deposits of ash beds, black shales, mudstones, and sandstones that represent a paleoenvironment with repetitive volcanic events from nearby shield volcanic complexes. Volcanic activity peaked at the time of the deposition of the Yixian Formation and dwindled through the time of the deposition of the Jiufotang Formation. The extensive sedimentary layers of lake mud and volcanic ash beds have yielded not only an exceptionally well-preserved treasure trove of feathered dinosaurs and early birds, but also equally magnificent assemblages of other vertebrates, including fish, amphibians, turtles, choristoderes, squamates, pterosaurs, ornithischians, and mammals, as well as insects and plant remains. These fossils represent one of the largest and most diverse collections of terrestrial vertebrates of any site in the world from the Cretaceous period and provide many missing links in evolutionary history. The most captivating part of the Jehol biota is the abundance of theropods and early birds with intact skeletons covered with incredibly delicate feathers of all stages, giving us a rare glimpse at the strange paths that theropod evolution took and how one of these paths led to creatures that still sit outside our windows to this day, merrily tweeting

Figure 1.1. Composite paleoecological reconstruction of the Jehol biota showing the transition from feathered coelurosaurs to early birds (or avialans) that lived in and around an ancient lake. The erupting volcano in the distance would recurrently kill and bury the Jehol community intact within ash beds. With rain the ash layer with the entombed Jehol community would turn into a muddy substrate (lahar deposit) and be transported to the lake bottom. There it would be preserved exquisitely as *konzentrat-lagerstätten* (German mining jargon for "motherload," meaning an anomalously high concentration of fossil material). Lagerstätten represent an extremely important window on the past, preserving innumerable taxa with soft tissues. The taphonomy (process of fossilization) of the Jehol biota indicates allochthonous deposits, meaning that animals were transported from their living sites during fossilization. In this reconstruction, only feathered coelurosaurs and avialans are pictured to show the evolutionary transition from theropods to early birds, frozen in the Early Cretaceous time. Feathered coelurosaurs 1–4): 1, *Sinosauropteryx*; 2, *Caudipteryx*; 3, *Sinornithosaurus*; and 4, *Microraptor*. Early avialans (5–8): 5, *Jeholornis*; 6, *Protopteryx*; 7, *Confuciusornis*; and 8, *Yanornis*.

away. It is these discoveries, fulfilling Darwin's dream of missing links, that excite both the paleontological community and the public.

Since the Jehol biota are embedded in fine-grained undisturbed lake sediments, some unusually delicate structures, such as the veins of leaves and insect wings, skin patterns, and the color and filaments of feathers are preserved in great detail. The Liaoning fossils are unique time capsules that capture Early Cretaceous ecology and diversity of life at a time when China was somewhat isolated from other continents (fig. 1.2). In this lakefront forest environment, small-feathered dinosaurs and their descendants—the early birds—lived and interacted together in amazing diversity and died together episodically in mass mortalities, as if their evolution and life history were frozen in time (Chang 2008). These finely laminated lake sediments record tranquil Jehol environments, which were episodically interrupted by volcanic ash falls, recurrent mass mortality events, and catastrophic floods, which may have been responsible for the preservation of the more spectacular components of the Jehol biota, such as feathered dinosaurs and birds.

Local farmers have dug up fish and insect fossils from the Liaoning site for decades to sell to collectors, but

the discovery of the first feathered dinosaurs (*Sinosauropteryx)* in the 1990s attracted worldwide attention that led to systematic excavation by Chinese paleontologists. The Jehol fossils are enclosed in gray volcanic ash that was deposited on the bottom of shallow lakes. The fossil remains come from several catastrophic events that are preserved layer after layer in a 1,600-meter-thick bed of sediment. It would take paleontologists several decades to uncover, retrieve, and understand the evolutionary impact of these buried treasures.

Taphonomy: Secrets of Death

Using combined evidence from sediments and fossils, paleontologists have reconstructed the ancient terrestrial ecosystem of the Jehol biota. The Early Cretaceous forests of Liaoning around lakes contained a variety of plants, including conifers, ginkgoes, horsetails, ferns, and early flowering plants that supported a variety of herbivores and insects. The landscapes, their flora, and their fauna were under constant threat from volcanoes, which periodically produced showers of toxic gas and suffocating ash, killing the organisms. The taphonomy, or death assemblage, of the Liaoning fossil site indicates that the animals died in recurrent catastrophes that caused the synchronous deaths of all members of the community. The Liaoning fossil site has been dubbed the "Cretaceous Pompeii" because the preservation of the Jehol biota by ashfall resembles that of the residents of Pompeii. Unlike the citizens of Pompeii, however, the denizens of Jehol were not killed instantly by lethal thermal impact. Most likely, these animals were caught by surprise when they were engulfed in an ominous cloud of ash from a nearby volcano, died of lung failure induced by inhaling ash and poisonous gas, and were buried instantly by the ashfall. Most skeletons show the onset of muscular relaxation, indicating that the Jehol animals experienced slower deaths than the people in Pompeii. Many animals were preserved in a sleeping or resting pose. Skeletons, delicate tissues of skin and muscle, feathers and their color pigments, undigested stomach contents, and eggs in oviducts were not carbonized and burned but preserved in exquisite detail, indicating that suffocation, not thermal impact, was the primary cause of the recurrent mass mortality of the Jehol biota. Rapidly accumulating ash, windblown into deep drifts at low-lying lake sites, remained relatively soft. The ash preserved the animals in three dimensions; not even the delicate bones of birds and pterosaurs or the wings of insects were crushed or burned. Such a catastrophe was so extensive that the animals had no opportunity to flee to a safe refuge but all died instantly—young and old, carnivores and herbivores, terrestrial and flying forms. These animals provide unusual and rare insights into the third dynasty of dinosaurs in the Cretaceous world, suspended in time and intact after 125 million years.

How did the remains of thousands of animals enter lakes intact with no evidence of disarticulation or the scattering of bones? The plant remains in the Jehol biota indicate that the climate fluctuated between being warm and humid and being hot, stormy, and wet. The ash beds probably derived from eruptions adjacent to lake basins. It appears that ash deposits covering the remains of terrestrial animals on lakeshores became unstable with torrential rains and turned into lahar avalanches, sliding islands of mudflow that cushioned and carried whole communities to the bottom of lakes, where death assemblages were rapidly buried, keeping the carcasses intact. Relative proximity to the lakes facilitated the transport of terrestrial vertebrate carcasses from a habitable environment to one that favored preservation by debris flow. The transported burial sites in lake bottoms, called allochthonous burial, aided by the low oxygen level that halted bacterial decay of soft tissues and deterred the scavenging of the corpses, sealed the dead communities forever for posterity. Low oxygen level at the lake bottom prevented bioturbations by worms and other invertebrates. Rapid deposition of ashes from airfall covered and protected the remains of the Jehol biota and provided an ideal environment for the preservation of death assemblages. After each volcanic disaster, life rebounded and Liaoning was populated again by a variety of animals and plants for some time until they were killed off by the next

eruption. The process of death and renewal continued for millions of years and was delicately preserved in the sedimentary layers of Liaoning (Chatterjee and Templin 2012).

The Cretaceous Park

I was a participant in the recent renaissance in Chinese paleontology. In 1985, I was invited by Dong Zhiming and Sun Ai-Lin of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), the premier scientific organization in Beijing, to lead a dinosaur expedition to Lufeng, a small village in China's Yunnan Province under the auspices of the National Geographic Society. Dr. Dong and his students accompanied us in the field. We discovered a series of complete skeletons of prosauropod and sauropod dinosaurs, crocodylomorphs, and mammals from the Early Jurassic Lufeng sediments. In the process we developed a close rapport, friendship, understanding, and collaboration with Chinese paleontologists. Since then I have worked with my Chinese colleagues and developed a genuine regard and admiration for their ingenuity and trailblazing work. In 2000, I was invited to present a paper at the Society of Avian Paleontology and Evolution (SAPE) conference in Beijing on the Antarctic fossil bird *Polarornis*, which we discovered from the frozen continent. After the meeting, there was a field trip to the famous Liaoning fossil site, about 650 kilometers northeast of Beijing (fig. 1.2A). We went to the paleontological field and examined some of the incredible bird fossils and their antecedents discovered by my Chinese colleagues from the IVPP. Looking at the extensive panoramic exposures of the Liaoning lacustrine ash beds, stacked beautifully layer upon layer like a valuable old manuscript, each layer containing an ancient treasure trove, I experienced an epiphany, a sense of awe and wonder, a recognition of something beyond the boundaries of human existence. Suddenly the whole Jehol forest community around the large lake came to life: little feathered dinosaurs and tiny mammals on tree branches, primitive birds and pterosaurs fluttering in the sky, large dinosaurs jostling on the ground, insects buzzing near the water surface, fish and amphibians swimming and splashing in the lake, and the first flowers blooming in the water. It was a wonderful experience of the lost world that became vivid to me.

Until recently, our knowledge of the Mesozoic radiation of birds and the evolution of their flight was based on a limited number of diverse Mesozoic taxa widely separated in time and restricted to marine environments. *Archaeopteryx* from the Late Jurassic Solnhofen Limestone of Germany was regarded as the Urvogel, the most primitive bird and the universal common ancestor from which all birds could be derived. *Archaeopteryx* has enjoyed this iconic position for the past 150 years. The recent burst of several dozen fossil discoveries of exquisite terrestrial birds from the Early Cretaceous Jehol deposits of China for the past two decades representing all lineages of early radiations of birds and the major steps in flight evolution have filled in major evolutionary gaps. The Mesozoic is no longer the "Dark Ages of Birds" with the discovery of Chinese fossils at an unprecedented rate, representing more than sixty species of all kinds of early birds—avialans, pygostylians, enantiornithines, and ornithuromorphs and their paravian ancestors. The sequence of alternating lacustrine and volcanic deposits provides an ideal setting for preservation of delicate bones and plumages of early birds and their ancestors in intact positions. The Jehol Group is also important because specimens from these deposits not only reveal size, anatomy, and flight adaptations, but also shed new light on other aspects of biology of extinct animals such as feathers, sex, diet, ecology, life history, and development.

In this book, I highlight some of the amazing Early Cretaceous birds and their Middle-Late Jurassic ancestors from China that were clothed with equally dazzling feathers. Here in this northeastern China, the evolution of birds and their flights have been frozen in exquisite detail in these thick ash beds spanning some 30 million years. It is difficult to keep up with ongoing new discoveries of Chinese birds and their antecedents unearthed from the Jehol graveyard almost at regular intervals. Thus the synthesis in this book can be summed up as a *work in progress*, as new discoveries in the future will certainly change the

topology of the avialan tree and fill important gaps in the narrative.

Two outstanding Chinese paleontologists, who introduced the Jehol feathered dinosaurs to the rest of the world by publishing their incredible papers in highly prestigious journals such as *Science* and *Nature* in collaboration with their colleagues, are Xu Xing and Zhou Zhonghe. In this book, the scholarly works of Xu Xing on feathered dinosaurs and Zhou Zhonghe on early birds will feature prominently in re-creating the lives of feathered dinosaurs and early birds, their phylogeny, and flight evolution.

The extraordinary preservation of the Liaoning fossils—far superior to that of other Lagerstätten deposits anywhere in the world—opens a new window on the ancient lifestyle of the Early Cretaceous dinosaurs and their contemporaries. Because of this globally outstanding paleontologic value, the Liaoning fossil locality has been inscribed as a new UNESCO World Heritage Site, having outstanding universal value for humanity. The life-and-death drama of the Early Cretaceous dinosaurs and birds is slowly unfolding from the Jehol ash beds because of the painstaking work of many paleontologists.

The most celebrated fossils from the Jehol biota include a series of feathered dinosaurs, spanning the phylogenetic transition from basal coelurosaurs to ornithurine birds that represent the critical stages for the origin and early radiation of birds. The Liaoning fossils indicate for the first time that feathers can no longer be used as a defining character of birds. Instead, their presence in small coelurosaurs reinforces the view that birds did indeed evolve from small theropods and that feathers evolved initially for insulation or sexual display and were later co-opted for flight, an evolutionary process called preadaptation or exaptation. Many of these small, feathered coelurosaurs had acquired several avian characters and are successively closer to early birds, thus narrowing the morphologic and phylogenetic gaps between these two groups (fig. 1.1). One of the most compelling evolutionary evidences from the Jehol coelurosaurs is the unique preservation of a diversity of primitive feathers and the progressive development of wing structures that provide critical clues to the origin of feathers and the evolution of avian flight. These feathers were colorful, dazzling, and iridescent and were used for sexual display and species recognition. These arboreal coelurosaurs opted for the flashiest feathers to compete for and obtain the best mates. Examples of Darwin's sexual selection are rampant in the Jehol and the older Daohugou fossil record. Later these feathers were modified and evolved for flight. Sex might be the primary driver for the evolution of birds from their feathered coelurosaurian ancestors with the development of powerful wings. The Jehol biota is replete with stories of sexual selection and evolution.

During the Early Cretaceous time, about 125 million years ago, Pangea began to rift and drift apart. At the time sea level was somewhat higher than it is today and shallow seas flooded the margins of the continents. The North Atlantic was closed, the South Atlantic was just beginning to open, and the southern continents of Gondwana had just begun to break apart. There was a large open Pacific Ocean that flooded the eastern seaboard of China. At the time, China was a collage of small continental blocks, which were separated by shallow seas. India was still attached to the southern continents. East and Central Asia maintained corridors with Europe for faunal exchange. Many of the vertebrates that originated in the Jehol biota spread to Europe and other continents. There were three major continental blocks in China—the North and South China Blocks, separated by the Qilian-Qinling-Dabie Mountains, and the Tarim Block. East Asia at the time was an island continent, a sort of ancient Australia, separated from the rest of the world. An active subduction zone on its eastern seaboard rimmed the margin with recurrent volcanic activity (fig. 1.2B). The Jehol locality at the time was located at paleoaltitude 40°–45° N, not far from its present position. The feathered coelurosaurs, early birds, pterosaurs, and mammals in China were "living fossils" in the Early Cretaceous ecosystem, evolving in splendid isolation as long-lived relicts and in isolated refugia. The isolation also encouraged geographic speciation and rapid diversification of animals and plants. Owing to this isolation, the Jehol biota consists of many endemic forms and primitive species, which are otherwise known from

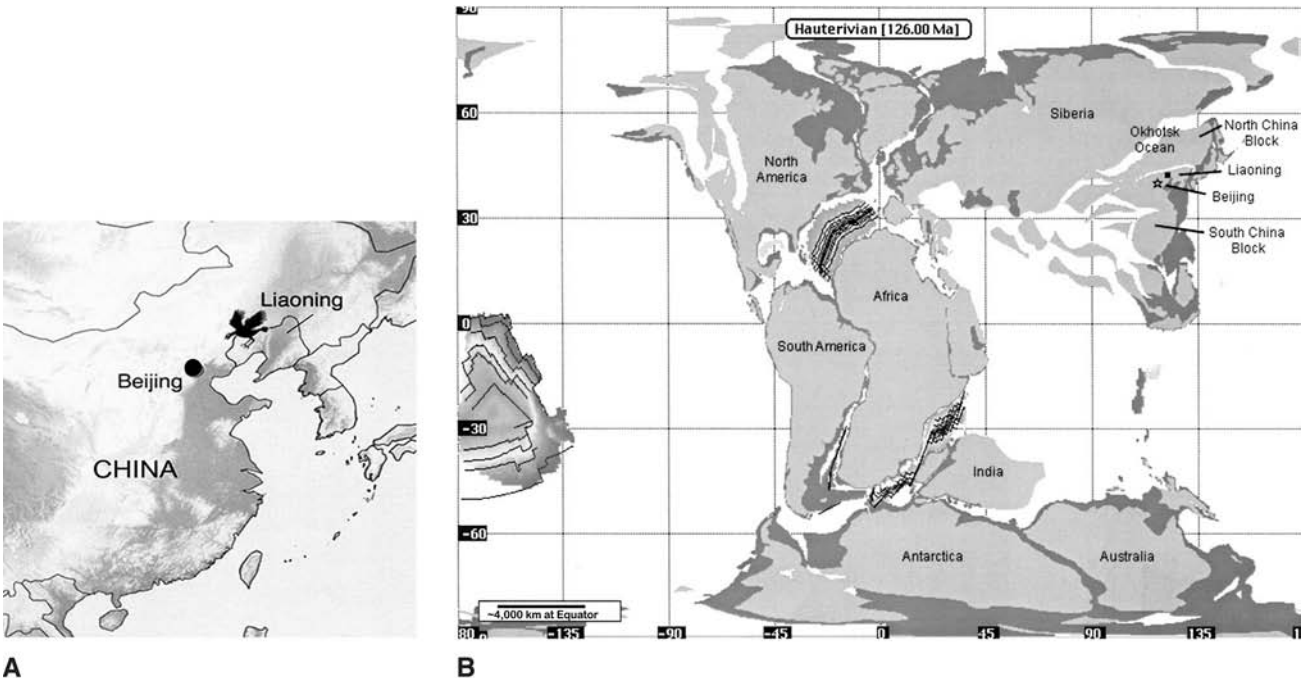


Figure 1.2. A, location of the Jehol biota in Liaoning Province in northeast China. B, plate reconstruction for the Early Cretaceous time showing the paleoposition of the North and South China Blocks and the location of the Liaoning fossils (after Chatterjee and Templin 2004b).

the Jurassic sediments of Europe. The Jehol biota provides a unique window on the origin of birds and their evolution of flight: why and how they acquired feathers and wings and when they began to fly. It has offered the best evidence for studying other groups of contemporary vertebrates such as fish, amphibians, reptiles, pterosaurs, and mammals, their anatomy and paleoecology.

A Pre-Jehol Mass Mortality Event: Daohugou Biota

A pre-Jehol biota of significant evolutionary importance, called the Daohugou biota, has been discovered recently in northeastern China. The fossiliferous Daohugou beds consist of thin-bedded lacustrine sediments intercalated with ash beds that occur around Daohugou village in Nincheng County, Inner Mongolia, in northeastern China and extend to Liaoning. Fossils come from two horizons, the older Jiulongshan Formation and the younger Tuchengzi Formation; both are highly folded and faulted. The Daohugou fossils were preserved in fine-grained lacustrine deposits similar to those seen in Jehol localities. The Daohugou biota is older than the Jehol biota by about 30 million years and is assigned to the Middle-Late Jurassic age (about 160 million years ago). The Daohugou biota and the Jehol biota are two successive Lagerstätten assemblages that occupied the same geographic region and collectively offer a glimpse of the rich Mesozoic life of China. Beautifully preserved fossils of ginkgos, cycads, horsetails, palms, insects, salamanders, anurans, dinosaurs, pterosaurs, and mammals have been discovered from these volcaniclastic rocks. Some of the remarkable fossil potpourris include feathered theropods such as flightless *Epidexipteryx*, and *Epidendrosaurus*, as well as *Xiaotingia*, *Pedopenna*, and *Anchiornis* with biplane wing planforms (see chapter 14); pterosaurs such as *Darwinopterus*, *Jianchangopterus*, and *Jeholopterus*; a gliding mammal such as *Volaticotherium* and the earliest placental mammal such as *Juramaia*; as well as an unusual feathered ornithischian *Tianyulong* (Liu et al. 2012). The paleoecology of the Daohugou biota is similar to that of the Jehol environment, where predominantly

gymnosperm forests flourished in a humid, warm temperate climate supporting a rich animal and plant community, which was recurrently engulfed by a cloud of ash or poisonous gas from a nearby volcano, leading to catastrophic death and burial. It was a prelude to the tragic Jehol episode of volcanic death. But life was tough and resilient and rebounded after each catastrophe with new vigor, as younger horizons of fossiliferous beds testify. The Daohugou fossils expand our knowledge about the early evolutionary stages of Jehol life, representing the beginnings of the Jehol radiation. Many of the Daohugou vertebrates represent the earliest record of their respective clades in the stratigraphic record. Since the Daohugou Formation is somewhat older than the *Archaeopteryx*-bearing Solnhofen Limestone of Germany, it provides a critical window on the earlier stages of bird evolution.

2 The Evolution of an Airframe

With his powerful wings he brought to man the oblation
loved by the gods.

Rig-Veda, ca. 1500 BC

Birds evolved from small, bipedal, feathered theropods, which changed their structure as they changed their habitat. The evolutionary transitions from feathered coelurosaurs to early birds are beautifully documented by extraordinary fossils in the Jehol and Daohugou biota, as discussed in the following chapter. From land, small theropods first moved to trees for safety from hungry predators, then learned how to live in a three-dimensional world, acquiring balance and coordination. From trees, they took to the air in small baby steps, first by parachuting, then by gliding, and finally by flapping and maneuvering. Forelimbs that had been used for catching prey on the ground were modified for climbing vertical tree trunks with clawed fingers, eventually morphing into wings for flight. Brilliant downy feathers that evolved initially to attract a mate and for species recognition developed into stiff contour feathers that were co-opted for flight.

Once started on an arboreal life, the theropod body was altered in more subtle ways. Climbing adaptation changed short forelimbs into elongated and powerful wings. The downy feathers that covered the body for insulation and sexual display were also gradually transformed, eventually becoming light, overlapping, stiff, and flexible contour feathers. The long theropod frame became a compact structure with a flexible neck, stiff trunk, strong ribcage and powerful shoulder girdle to support a body suspended from wings. Finally, in arboreal life, where coordination and sharp vision are crucial to survival in a three-dimensional world, the bird's brain expanded in a lighter skull. The Jehol and Daohugou biota offers crucial insights about the ecology and the evolution of the skeleton of modern birds from that of their theropod ancestors.

All birds have an internal bony skeleton that provides support and keeps the body from collapsing. The bones interconnect at joints; most joints are mobile, but some are fixed. Between mobile joints, the bones are rigid and serve as levers across which the muscles can act. Bones support the muscles used in locomotion, other body movements, and posture; they protect such internal organs as the brain, heart, and lungs; they also house bone marrow, which produces blood. Bone is composed of hydroxyapatite, a hard and durable material that changes little with fossilization and thus provides important clues to vanished soft parts. Tuberosities, depressions, and scars on bones reveal the positions, sizes, and attachments of muscles. The endocranial cavity and cranial

nerve foramina reveal the size of the brain and the distribution of the neural network, and the nasal cavity, orbits, and otic capsules provide information about the size and orientation of the sense organs. Teeth, claws, limbs, and girdles are all coordinated with feeding habits and methods of attack and defense, including posture and locomotory patterns. Bones let us see the time dimension in the evolution of vertebrates and, in particular, the rise of birds.

Like any flying machine, birds must possess two basic attributes to defy gravity: a light, strong structure and efficient power. To minimize weight and maximize power, bones and muscles have been modified. Most bird bones are hollow, light, air filled, and often stiffened internally by struts. Fusions and reinforcements of lightweight bones make the avian skeleton both powerful and delicate. Air spaces in the wing bones link up with the lungs through a network of air sacs to form an extensive combined respiratory and cooling system. The heavy bony jaws filled with dense teeth in ancestral theropod dinosaurs were replaced by the lightweight, toothless bill in modern birds. Many bones and the long, cumbersome bony tail were eliminated to reduce weight and improve flight; other bones normally sutured were fused for strength and rigidity. The forelimbs and the shoulder girdle were modified into a flight apparatus, and streamlined, strong, and flexible feathers provided lift and propulsion. The fully ossified dorsal and ventral ribs of the thorax, the strong shoulder girdle, and the keeled sternum provide a strong framework to withstand the strains imposed by the flight stroke (fig. 2.1). The lightweight bird skeleton is a minimalist design in excellence, eliminating all nonessential structures and retaining only those critical parts necessary for flight and survival.

Flight is a demanding method of locomotion that requires a great deal of power. This power is provided by two sets of flight muscles, which contract alternately to flap the wings. The collapsible wing supports flight feathers, and the keel of the sternum anchors the powerful flight muscles, which make birds not only enduring fliers but also the swiftest of all animals. A bird must be as light as possible, and flight is more manageable if the remaining weight is concentrated near the center of the body. This is achieved by rearrangement of the internal organs, elimination of some organs, and rearrangement of the posture.

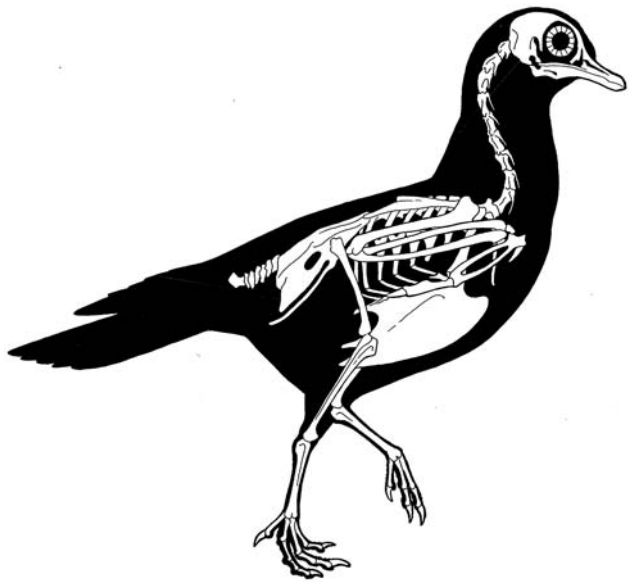


Figure 2.1. Lateral view of the skeleton of a pigeon (*Columba livia*) showing the light and rigid airframe for flight. Many avian features in the skeleton are visible, such as the kinetic skull; fused bones in the skull, thorax, sacrum, pelvis, carpometacarpus, tibiotarsus, and tarsometatarsus; a flexible neck; a short tail with a pygostyle; a large, keeled sternum; and wings.

Theropod Heritage

The primary adaptation that established birds as a clade was flight. Virtually every distinctive characteristic of bird anatomy has evolved as an adaptation for flying. The skeletal similarities between early birds and theropod dinosaurs leave no doubt about their evolutionary relationship. We want to know which theropods gave rise to early birds, and how the transformation proceeded. It has long been accepted that the Late Jurassic *Archaeopteryx* from Germany was a transitional form between birds and reptiles, and that it is the most primitive basal bird—the Urvogel. It is not thought to be a true ancestor of modern birds but, rather, a close relative of that ancestor, a living fossil in the Jurassic world. *Archaeopteryx* bears more resemblance to its ancestors, the drom-

aeosaurs, than to modern birds, providing a strong phylogenetic link between the two groups. Unlike modern birds, *Archaeopteryx* had small teeth as well as a long bony tail, features that it shared with other dromaeosaurs of its time. Currently, *Archaeopteryx* is included in the clade Avialae, which contains the living representatives of birds and their most immediate extinct relatives.

However, the avialan status of *Archaeopteryx* has been challenged recently (see chapter 4). The discoveries of numerous small, feathery coelurosaurs in China have created a conundrum for paleontologists, raising questions about which theropods are the ancestors of modern birds and which are just closely related cousins. The recent Chinese fossil that shook the base of the bird family tree and knocked *Archaeopteryx* from its perch is *Xiaotingia* from the Middle-Late Jurassic of China. *Xiaotingia*, which is not a bird, is found to be a close relative of *Archaeopteryx*. As a corollary to this new relationship, *Archaeopteryx* may not be a bird at all, but may lie in a sideline of theropod radiation as a member of the deinonychosaurs along with *Xiaotingia* (Xu et al. 2011). Another Chinese bird, *Jeholornis*, is ready to take the position of Urvogel, displacing *Archaeopteryx* from its iconic status, as discussed later. This view has been supported by more recent analysis that removed *Archaeopteryx* from the base of birds and put it back with the deinonychosaurs (Godefroit et al. 2013a). However, a follow-up study has reinstated the avialan status of *Archaeopteryx* (Godefroit et al. 2013b). Whether this change is permanent depends on what other basal birds are discovered in the future. Taxonomic uncertainties about the flip-flop status of *Archaeopteryx* are not new; they began since its discovery about 150 years ago, vacillating between theropod and early bird. Whether *Archaeopteryx* is a true bird or not, it provides a good bauplan, a basic design of how the primitive bird would look. Until the controversy is settled, the anatomical transition from dromaeosaurs to modern birds provides a reasonable road map to understanding the major stages of the evolution of avian skeleton.

The skeleton of the small dromaeosaur is designed for running and climbing. Dromaeosaurs share several features with birds, including a large braincase, large orbits, elongated forelimbs, swivel wrist joints, tridactyl manus, a large pelvis, a reverted pubis, obligatory bipedal posture, and scansorial (climbing) locomotion (Ostrom 1976a). The hands and wrists of dromaeosaurs are so similar and avialan in their shape that the arms were normally held in a folded position, like the wings of a bird. A detailed comparison of the skeletons of dromaeosaurs and birds shows the closeness of these two groups (fig. 2.2). From the dromaeosaur body plan, the avialan skeleton has undergone drastic evolutionary modifications related to flight adaptation. Comparative anatomy provides important clues to the evolution of the airframe.

Figure 2.2 compares the skeletal features of the pigeon (*Columba livia*) and other recent birds with those of dromaeosaurs to highlight these evolutionary modifications into an airframe. Once we understand these skeletal changes between the beginning and end points of avian evolution, the sequence of acquisition of avian features in Mesozoic birds can be traced.

The Skull

The avian skull is modified greatly from the dromaeosaurid design in response to three functional requirements: (1) flight; (2) enlargement of the brain; and (3) the ability to move the upper jaw, which is linked to altered feeding habits. The skull is lightly built and aerodynamically designed. The pointed beak and rounded braincase act as an airfoil. Thinning of the compact layers of the dermal bones has reduced the weight of the skull, but the skull remains strong because sutures are fused in adults. Some skull bones have been reduced or lost. The spherical braincase is the optimum shape for holding a highly enlarged brain. The orbits, large depressions on the spherical braincase, accommodate enormous eyes. Birds differ from dromaeosaurs in being able to move the upper jaw relative to the braincase. The triangular, pointed beak is mobile and is an efficient food-gathering device.

The skull of a young chicken (*Gallus gallus*), in which the sutures are still open, can be compared with that of *Dromaeosaurus* to trace the architectural changes. The most distinctive departure from the dromaeosaurid skull pattern is the large orbit and the inflated braincase in

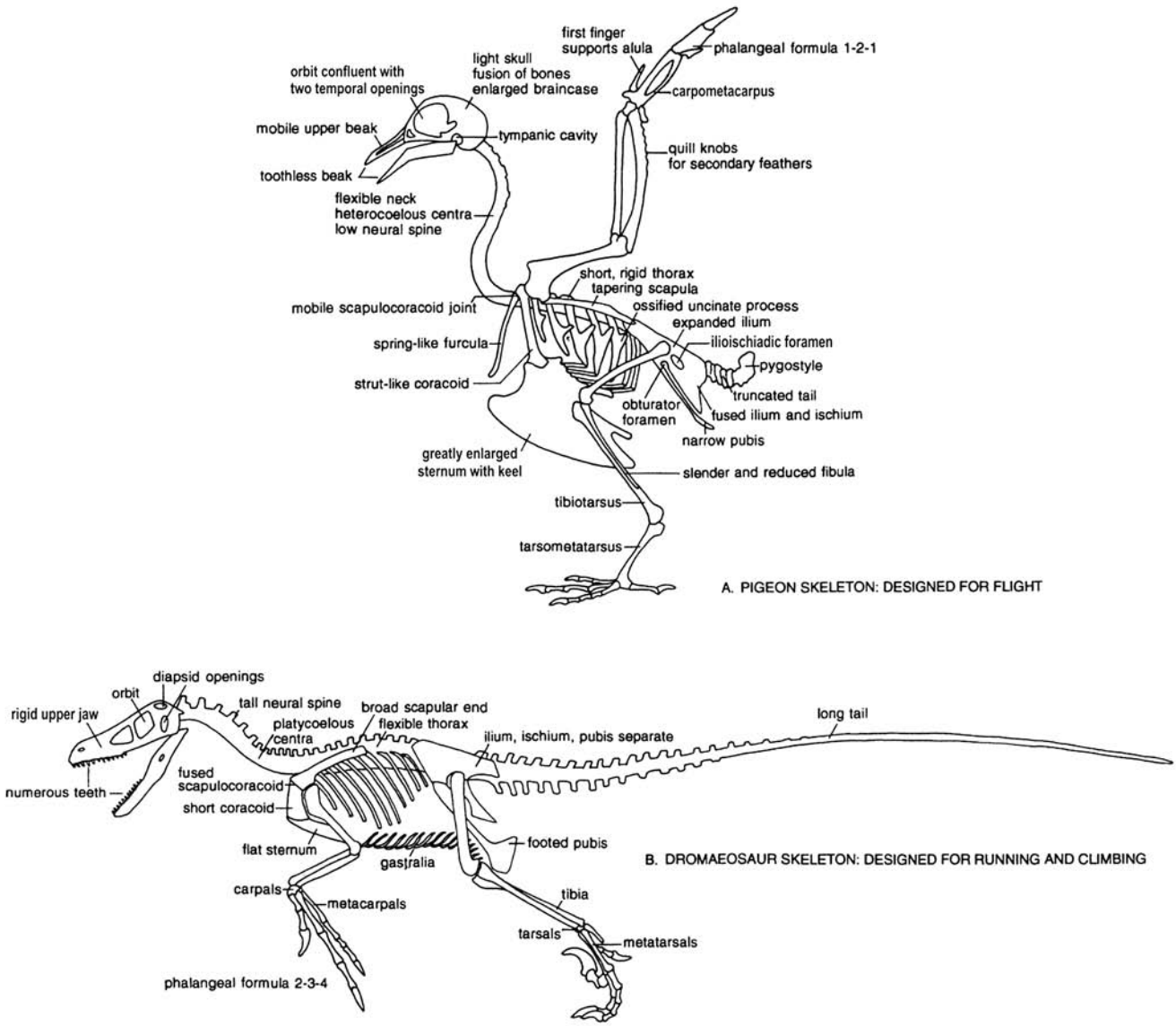


Figure 2.2. Comparison of the skeletons of a pigeon and a dromaeosaur to show the similarities and differences. Many avian features evolved from a dromaeosaur-like body plan in response to flight adaptation in birds. A, the skeleton of a pigeon in the left lateral view; B, the skeleton of a dromaeosaur in the left lateral view; both A and B are semidiagrammatic.

birds. These modifications become clear when we compare the side view of the skull, especially in the cheek region (fig. 2.3A–B). The postorbital bone and the ascending process of the jugal behind the orbit and between the two temporal openings have disappeared in birds so that the orbit becomes confluent with the two temporal openings. The merger of these three openings gives a very large space for the enormous eyeball, which provides bigger and sharper images. Visual information is extremely important to birds. Another diapsid arch, the squamosal-quadratojugal bar in front of the quadrate, is also eliminated. The freed quadrate becomes mobile, or streptostylic. The teeth are lost so that the jaws become lightweight struts to support the horny upper and lower beaks. The gizzard in the stomach takes on the role of teeth for processing food.

With the loss of the postorbital bone, two important landmarks are visible on the sidewall of the skull behind

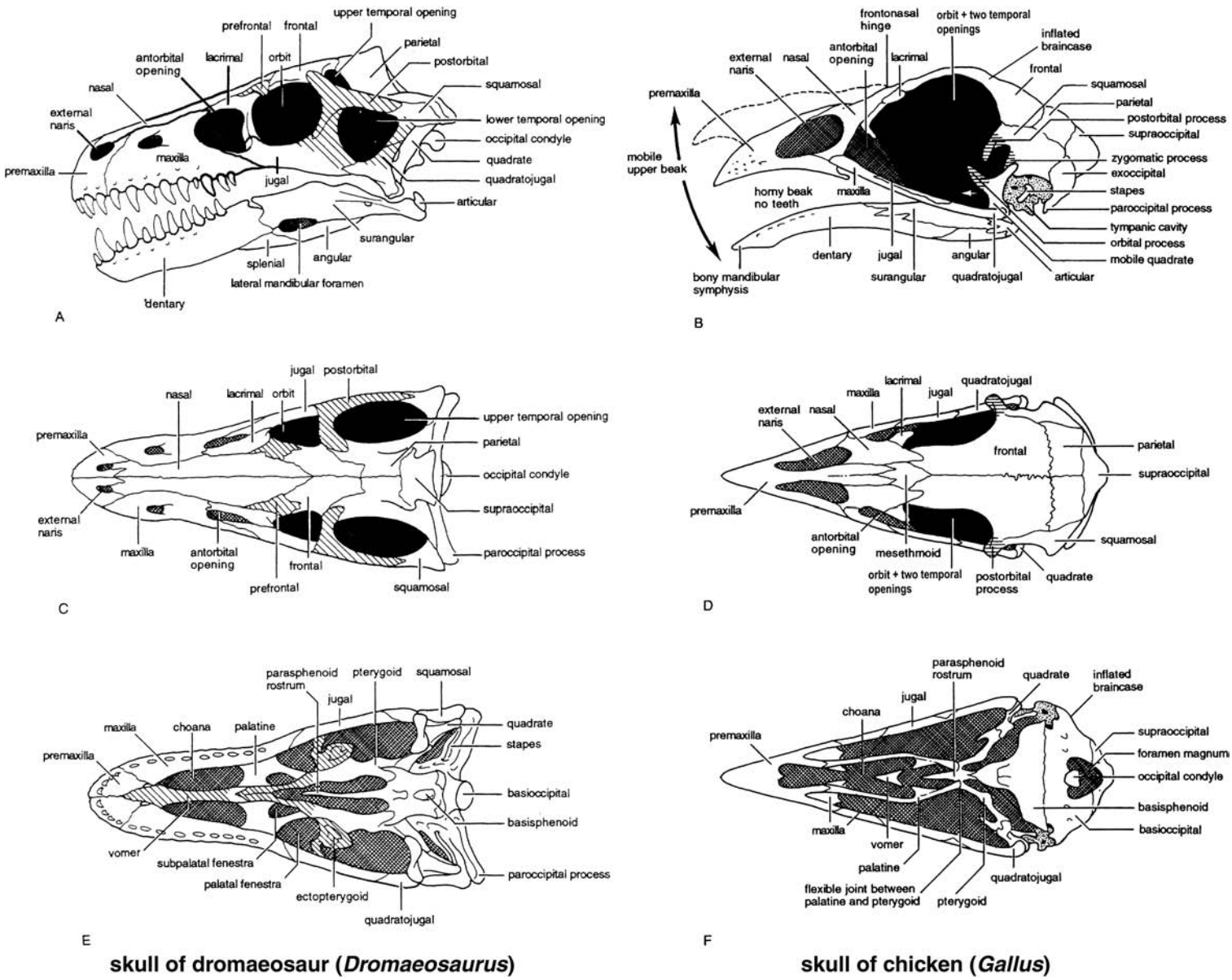


Figure 2.3. Comparison of the skull of a dromaeosaur and a bird (chicken). The most important anatomical innovation in birds is the modification of the temporal region of the skull, where the orbit becomes confluent with the upper and lower temporal openings. This modification allows birds to raise their upper jaws. A–B, lateral view; C–D, dorsal view; E–F, ventral view. Bony regions lost in the transition from dromaeosaur to bird skull are represented by diagonally shaded areas (A, C, E); new avian features, such as the postorbital process, zygomatic process, and orbital process, are represented by horizontally shaded areas (B, D).

the orbit: (1) the postorbital process formed by the frontal and the laterosphenoid and (2) the zygomatic process of the squamosal overhanging the quadrate (fig. 2.3B). The quadrate is greatly modified in birds. Its dorsal head is expanded medially to make an additional contact with the braincase. Medially, near its ventral margin, it receives the pterygoid in a ball-and-socket joint. As a result, it develops a distinct orbital process that acts as a muscle lever. Another bone, the prefrontal, is lost in birds, while the descending process of the lacrimal is reduced to breach

the contact with the jugal. With the breakdown of various vertical struts, the conjoined maxilla, jugal, and quadratojugal becomes a thin horizontal rod, the jugal bar.

In the dorsal aspect, a noticeable change is seen around the frontonasal hinge. The premaxilla and the frontal become large enough to approach each other along the midline so that the nasal bones are displaced laterally. The nasal bones become very thin and pliable where they contact the frontal bones. Here a new bone, the mesethmoid, is ossified to form a pivot at the frontonasal hinge (fig. 2.3C–D).

In the palatal aspect, the ectopterygoid is lost to free the pterygoid from the jugal. The choana is displaced caudally to merge with the palatal fenestra and forms an extensive cleft down the midline. The vomer is atrophied to a sliver of bone, and the palatine is elongated at the expense of the pterygoid. An additional movable joint is established between the pterygoid and the palatine in neognathous birds (fig. 2.3E–F). With the loss and reduction of some bones and the development of a median cleft, the avian palate becomes a delicate, springy framework.

The bird brain has enlarged backward and downward so that the foramen magnum is shifted from the occiput to the ventral side of the skull. Viewed from the ventral aspect, the occipital condyle is visible as a small spherical knob. Anterior to the condyle lies the highly expanded basisphenoid. The enlargement of the brain gives a dome-shaped appearance to the braincase. Some of the dorsal roofing bones, such as the frontal, parietal, and supraoccipital, become inflated to accommodate the large brain. Because of the backward protrusion of the braincase, a large tympanic cavity is created behind the quadrate for the external ear. From the lower and rostral part of the tympanic cavity, a funnel-shaped depression leads to the bony eustachian tube. The inner ear has an elongated cochlear process and enlarged canalicular system for refined hearing and balance.

All six bones in the dromaeosaurid mandible—the dentary, splenial, angular, surangular, prearticular, and articular—are recognized in juvenile birds, but their identity is lost in adult birds. With the loss of teeth, the lower jaw becomes a shallow, delicate structure. The notable change is the development of an ossified symphysis at the dentary to give strength and rigidity to the lower beak.

The Vertebral Column

The vertebral column of a bird has been modified considerably from the dromaeosaurid design. The number of neck vertebrae increased at the expense of the dorsal vertebrae; the thorax became a small, rigid box; the synsacrum (a solidly fused series of vertebrae in the pelvic region) was strengthened by the incorporation of more vertebrae; and the long bony tail was reduced to a few caudals and a pygostyle (a bony plate at the end of the spine). In dromaeosaurs, the cervical centra are platycoelous (slightly hollowed), with well-developed neural spines. In birds, the neck shows extreme mobility in all directions, with the development of heterocoelous (saddle-shaped) centra (fig. 2.4A–F). This long and flexible neck supports an elevated head, so that the beak can be used as a "universal tool." The neural spines are weakly developed in the cervical vertebrae. Behind the axis, the cervical ribs are short and fused with their vertebrae to enclose the canal for the vertebral artery. Ventrally, each centrum bears a pair of projections, or hypapophyses, which may also be fused into a single median ridge.

Fusion of two segments of the vertebral column behind the neck provides stable platforms for the shoulder and pelvic girdles, respectively. Because the thorax forms the fulcrum on which the wings move up and down, it must be short and rigid. The thoracic vertebrae bear complete ribs with uncinate processes, and each process overlaps the next posterior rib to strengthen the rib cage (fig. 2.1). The gastralia are absent in modern birds but retained in ancestral forms. The neural spines of the thoracic vertebrae are long and are often fused together, except between the hindmost, where there is some flexibility. Bipedal locomotion and the role of the hindlimbs as landing gear require a strong synsacrum. The synsacrum in birds is extensively developed from the dromaeosaurid condition by the incorporation of additional segments of posterior dorsals and anterior caudals. Moreover, both the transverse processes and the neural spines also brace the iliac blade. Following the synsacrum are six or seven movable

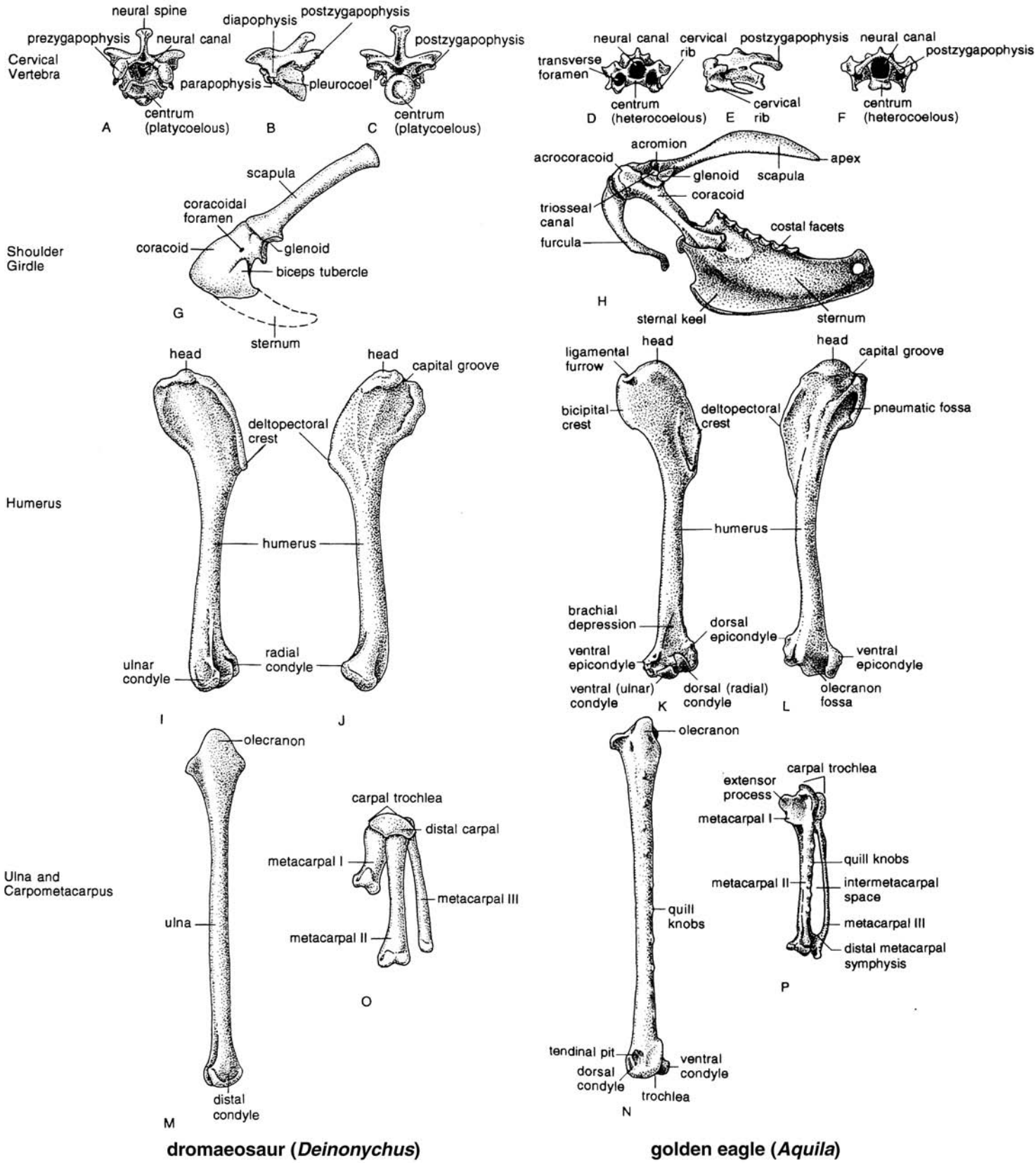


Figure 2.4. Comparison of the vertebrae (A–F), shoulder girdle (G–H), and forelimbs (I–P) of a dromaeosaur (after Ostrom 1969; courtesy of the Peabody Museum of Natural History, Yale University) and a bird (golden eagle) to show the similarities and differences.

caudal vertebrae that steer the tail for flight and maneuvering. The reduction of the long caudal series and the development of the pygostyle are new features in birds. The pygostyle supports the lightweight tail feathers.

The Shoulder Girdle

The shoulder girdle is perhaps the most distinctive feature of the avian skeleton and is built strongly to execute the flight strokes. In dromaeosaurs, the coracoid is relatively small and fused with the scapula to form the glenoid, which faces caudally (fig. 2.4G). The coracoid has developed the biceps tubercle, which may be the precursor to the avian acrocoracoid process (Ostrom 1976b). In birds, the coracoid becomes massive and strut-like to brace the sternum so that it can support the compressive force of the downstroke during flight (fig. 2.4H). The coracoid articulates with the scapula at an acute angle in a flexible joint. The glenoid fossa has been shifted outward and upward to permit the dorsoventral excursion of the humerus. Dorsally, the coracoid develops the acrocoracoid process to complete the opening for the triosseal canal in conjunction with the scapula and the furcula. This canal acts as a pulley, allowing the supracoracoideus muscle to raise the wing. This coracoideus pulley, a major innovation in birds, is used to execute the upstroke. The scapula, a narrow, tapering blade lying parallel to the thorax, reaches almost to the pelvis. The sternum is greatly enlarged and has a prominent keel ventrally for the attachment of large flight muscles. The V-shaped furcula is long, thin boned, and united ventrally at an acute angle. It acts as a flexible spring between the two shoulder joints during flapping flight (Jenkins et al. 1988). The furcula was recently discovered in an articulated skeleton of *Bambiraptor*, a dromaeosaur from Montana (Burnham et al. 2000). The sternum of dromaeosaurs is a flat bone like that of flightless birds, without any ventral keel.

The Forelimb

Major modifications of the forelimbs of birds include restriction of the movement of the elbow and wrist joints to one plane, reduction of the number of digits, loss of functional claws, and fusion of the carpometacarpus. In dromaeosaurs, the humerus is longer than the ulna. Moreover, the proximal and distal expansions of the humerus are twisted at an angle (fig. 2.4I–J). In birds, the humerus is shorter than the ulna and the terminal expansions lie in the same plane. Another departure in birds is the development of the bicipital crest and the pneumatic fossa at the proximal end. Unlike dromaeosaurs, birds have distal condyles that are well defined and a radial condyle with a circular profile (fig. 2.4K–L). The radius and ulna are joined with the humerus and the manus in such a way that the wrist and elbow joints are automatically coupled, allowing folding and unfolding of the wings. The ulna is also distinctive in many birds; a series of quill knobs lie on the outer surface for the attachment of the secondary feathers (fig. 2.4N). Moreover, the distal end has a trochlear surface for articulation with the ulnare. The proximal carpal bones—the radiale and ulnare—are well developed and complex in birds to play important roles in supporting and controlling wing movements (Vasquez 1992). In dromaeosaurs, the two distal carpal bones, distal carpal 1 and 2, often fused to a compound bone, the semilunate carpal. It shows a pulley-like surface, the carpal trochlea, on the proximal end, allowing restricted movement of the wrist joint at the plane of the forearm (fig. 2.4O). This swivel joint at the wrist helps to fold and unfold the hand at the side of the body when not in use. This joint is more refined in modern birds. However, the carpal and metacarpal bones of dromaeosaurs remain free. In birds, distal carpal 1 is lost. Distal carpal 2 and three metacarpals (I–III) are fused into a single bone, the carpometacarpus (fig. 2.4P). Like dromaeosaurs, birds have three digits, but the number of phalanges has been considerably reduced from the primitive pattern of 2-3-4-x-x. The phalangeal formula code is after Padian (1992); "0" indicates metapodials supporting no phalanges, and "x" indicates digits that are completely lost.

The Pelvic Girdle

In dromaeosaurs, three pelvic bones—the ilium, ischium, and pubis—remain free. The pubis is highly elongated and somewhat rotated backward, and it develops a large

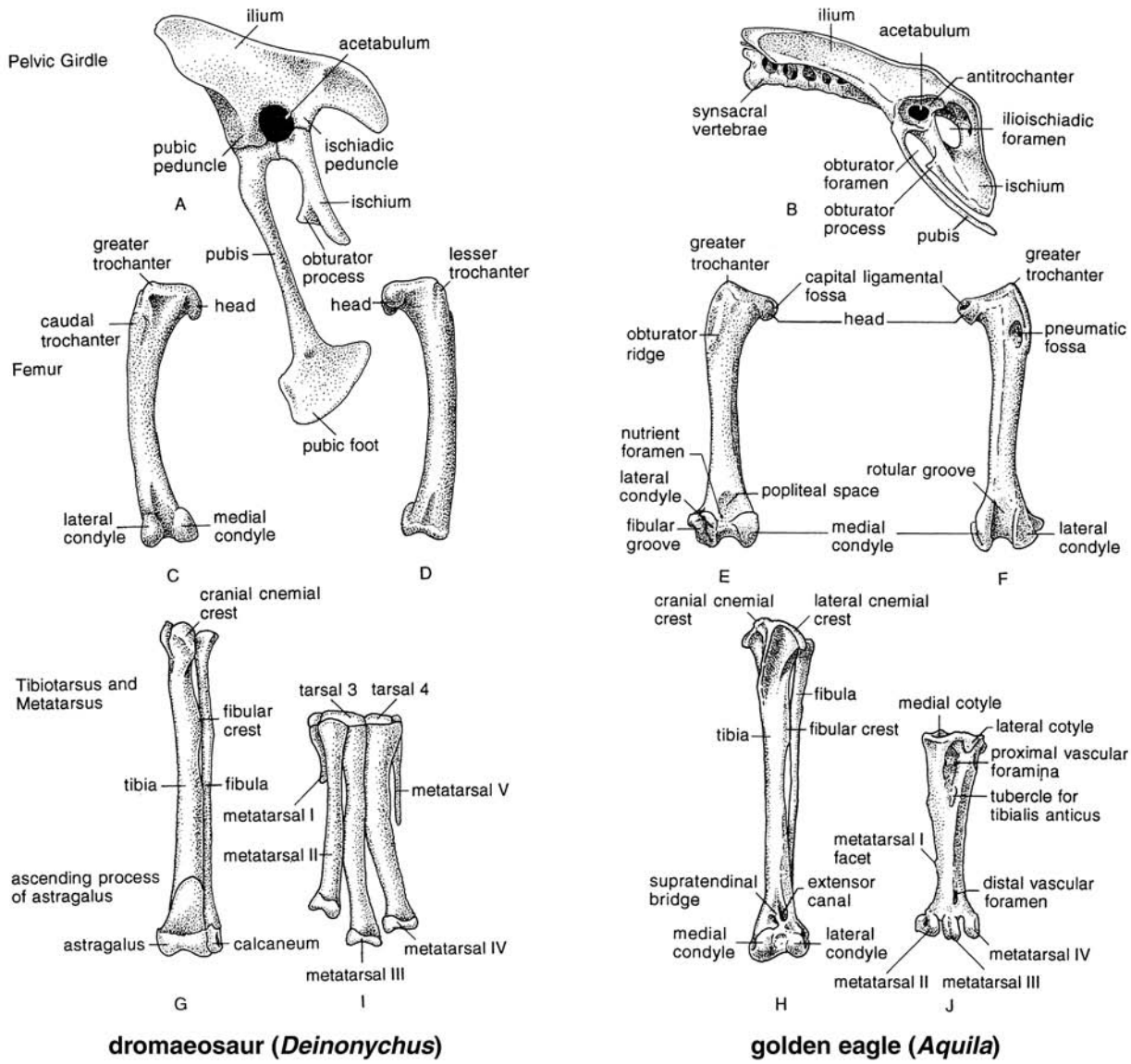


Figure 2.5. Comparison of the pelvis (A–B) and hindlimbs (C–J) of a dromaeosaur (after Ostrom 1969, 1976c; courtesy of the Museum of Comparative Zoology, Harvard University) and a bird (golden eagle) to show the similarities and differences.

foot at the distal end (fig. 2.5A). In birds, the pelvic girdle is formed by the fusion of these three bones with the synsacrum and shows extensive remodeling of the dromaeosaurid design (fig. 2.5B). The avian pelvic girdle is greatly expanded to provide a large area for the attachment of hindlimb and abdominal muscles. The ilium is elongated craniocaudally and is strongly fused with the synsacrum to form a rigid structure. Cranially, the two ilia approach each other to form a broad pelvic shield. The ischium, in turn, is fused with the ilium but is interrupted by the ilioischiadic foramen. The pubis is reduced to a thin and narrow strip of bone, rotated backward to run along the ventral edge of the ischium. Cranially, it is fused with the ischium, but is separated by the obturator foramen more distally. A secondary articulation between the femoral head and the acetabulum, the antitrochanter, prevents abduction of the femur. It also permits the legs to be tucked against the body for flight. A large renal fossa on the me-

dial surface of the ilium and ischium houses the kidney. In the bird, unlike the dromaeosaur, the two halves of the pelvic girdle remain open, without any symphysis.

The Hindlimb

Because the hindlimb is used for bipedal walking and leaping in both birds and dromaeosaurs, the structural differences between these two groups are not pronounced. There are, however, subtle changes in limb position and movement in birds. In dromaeosaurs, the femur moves in a nearly vertical plane at the hip joint during locomotion. Various subsidiary trochanters, such as the fifth and lesser trochanters, are eliminated in birds (fig. 2.5C–D). In birds, the femur is kept subhorizontally and is tucked away under the feathers; the main functional movement has been shifted from the hip to the knee joint. The femur shows some novelties, such as the elevated crest of the greater trochanter and the capital ligamental fossa in the proximal end, whereas distally it develops deep rotular and fibular grooves (fig. 2.5E–F). In dromaeosaurs, the tibia is locked with the astragalus and calcaneum without any fusion (fig. 2.5G). In birds, the tibia is fused with the astragalus and calcaneum to form the distal condyles of the tibiotarsus (fig. 2.5H). Here, it develops a supratendinal bridge over the tendinal groove. Proximally, it shows both cranial and lateral cnemial crests; the former is an avian innovation. The fibula is greatly atrophied and consists of a slender spicule of bone that fails to reach the ankle. In dromaeosaurs, the five metatarsals are present and remain separate from the distal tarsals. In birds, the distal tarsals are fused with metatarsals II, III, and IV to form a long, rigid, single bone—the tarsometatarsus (fig. 2.5J). Metatarsal I is reduced and articulates with metatarsal II distally; metatarsal V is lost. Proximally, the tarsometatarsus has one or more protrusions, the hypotarsus. The pes becomes anisodactyl—the first digit points backward to form a grasping organ for perching.

The Skeletomuscular System

The framework or the supporting structure of birds that maintains the shape of the body and makes it function well is provided by the skeletomuscular system. It can be divided into three distinct anatomical modules that operate independently: a head-neck module for feeding; a wing-tail module for flying; and a pelvic-hindlimb module for terrestrial locomotion and landing. Since birds do not use their hands for feeding, the highly mobile neck in concert with the head function as the main modular unit to procure food. Locomotor modules work independently in birds—the combined wing-tail module for flying and the pelvic-hindlimb module for walking or running. When birds fly, they use their wings and tail in concert for maneuvering, while their hindlimbs become disengaged from locomotion and are tucked behind or closely folded for streamlining. When walking or running, birds use their hindlimbs only, keeping their wings tucked tightly sideways. The skeletomuscular system of birds is an engineering marvel, improved through millions of years of experiments and natural selection as discussed in the following chapters.

3 The Origin of Birds

It took the whole of Creation
To produce my foot, my each feather:
Now I hold Creation in my foot.

Ted Hughes, *Crow*, 1960

Glorified Reptiles

Birds, which took to the air during the age of the dinosaurs, are unique and distinctive among living vertebrates because of their wings, feathers, and graceful flight. They are traditionally classified as Aves, a class separate from the rest of the vertebrates, such as fish, amphibians, reptiles, and mammals. Feathers and aerial prowess conceal the true identity and ancestry of birds. Natural selection has given them an edge by creating a lightweight skeleton, an aerodynamic coat of feathers, powerful wings, and highly efficient metabolic and respiratory systems that allow them to defy gravity and fly. A bird is an animal, made of bones, muscles, and feathers, heavier than the air through which it has to move. Wings and feathers have given birds the ability to rise into the air against the downward pull of gravity, move rapidly from one place to another, travel long distances, and find food. Yet their basic body plan bears their unmistakable reptilian heritage. What is the phylogenetic position of birds among reptiles? Who were their immediate evolutionary ancestors?

The question of the origin of birds has been one of the most contentious issues in evolutionary biology and has been debated for more than 150 years since the discovery of *Archaeopteryx* from the Late Jurassic of Germany. The origin of birds has often been equated with the origin of *Archaeopteryx*. Superficially, birds with their wings, feathers, flight, light and strong skeletons, hollow bones stiffened with struts, heterocoelous vertebrae, agility, acute vision, warm bloodedness, and specialized breathing system make them a distinctive class from all other vertebrates. Beneath the feathery coat, however, the true identity and reptilian heritage of birds are preserved in their bones, body plan, and DNA. Birds are archosaurian reptiles, as birds and reptiles share a unique feature in the skull—an antorbital fenestra in front of the orbit. Molecular phylogeny tells us that crocodiles and birds, the two extant groups of archosaurs, split at the base of the Triassic, around 240 million years ago (Kumar and Hedges 1998). Thus it is remarkable that soon after the discovery of *Archaeopteryx* the evolutionary link between birds and reptiles was instantly recognized. *Archaeopteryx* was a perfect transitional form between reptiles and

birds. It is often referred to as the Urvogel, the German word for "original bird" or "first bird." Recent discoveries, however, made scientists rethink the iconic status of *Archaeopteryx*.

Historical Debate over Bird Origins

In 1859, Charles Darwin published his monumental book *On the Origin of Species*, which provided a natural mechanism to explain the evolution of life through time. He proposed that all species of life have descended over time from a common ancestor. Evolution was struggling to find a foothold as a credible theory, and *Archaeopteryx* was the first solid anatomical evidence to back up Darwin's claims. Thomas Henry Huxley (1868a, 1868b, 1870), often known as Darwin's "bulldog" because of his fervent support of Darwin's new theory of evolution, seized on *Archaeopteryx* from the Solnhofen Limestone of Germany as a "missing link" between birds and reptiles, implying that birds evolved from reptiles, especially from dinosaurs. Like reptiles, *Archaeopteryx* retained teeth, clawed forelimbs, and a long bony tail. Like birds, *Archaeopteryx* possessed wings with flight feathers, a large brain, and perching feet. Huxley argued that a small coelurosaurian theropod such as *Compsognathus* from the same Solnhofen deposits as *Archaeopteryx* shows stunning skeletal similarities with *Archaeopteryx*, especially in their morphology of hindlimbs and girdles as well as their acquisition of bipedal posture, erect gait, and mesotarsal ankle joints. Huxley thus proposed the theropod origin of birds on the basis of these shared derived characters in the hindlimbs between the two groups. For several decades the famed Eichstätt specimen of *Archaeopteryx* lacking feather impressions was mistakenly identified as a juvenile *Compsognathus*, indicating how alike these two genera are in skeletal morphology as Huxley proposed (fig. 3.1A, B). The fact that theropods and birds always walked bipedally is intriguing and may indicate a common evolutionary history, Huxley argued. Bipedalism is a rare evolutionary event in the history of vertebrates and requires a great degree of balance and coordination. Huxley also noted that both theropods and juvenile birds possess a mesotarsal ankle joint with a distinctive ascending process on the anterior face of the astragalus that wraps the tibia for firm articulation (fig. 3.1C–E).

Huxley reasoned that if birds had not been so outstandingly successful in aerial adaptation, they would now be regarded as an order of reptiles, more specifically, a group of theropods, not a separate class of vertebrates. He thus coined a provocative genealogical term for birds, calling them "glorified reptiles," thus establishing a close evolutionary link between theropods and birds. Since then, *Archaeopteryx* has become central to the understanding of the evolution of birds and their flight.

In 1926, however, Gerhard Heilmann rejected the theropod hypothesis and proposed an alternative thecodont ancestry of birds. He argued that such small theropods as coelurosaurs, however bird-like in skeletal morphology, could not be considered ancestors of birds because they presumably lacked clavicles (collarbones), from which birds derive their furcula, or wishbone. Heilmann was guided by Dollo's law of irreversibility, which was popular at the time: if a structure had been lost during the course of evolution in ancestral forms, the descendants could not regain it. In other words, evolution does not backtrack to recover lost characteristics. For birds to evolve from theropods, the lost furcula would have to reappear. Faced with such a paradox, Heilmann made a reasonable compromise. He argued that both birds and dinosaurs had evolved from a common ancestor. He sought the common ancestor among bipedal thecodont reptiles, a mixed bag of Triassic archosaurs such as *Euparkeria* and *Ornithosuchus*, which retained the clavicle (fig. 3.2). From this ancestral stock, two great evolutionary lineages diverged, one leading to dinosaurs and the other to birds, Heilmann argued. For the next fifty years, Heilmann's thecodont hypothesis enjoyed wide acceptance among paleobiologists, with some new variations such as the crocodilian origin of birds.

Today, with refined techniques of biological classification such as cladistics and more and more discoveries of archosaur fossils, Heilmann's thecodonts are no longer recognized as a clade but as a paraphyletic group, a mixed assemblage of primitive archosaurs. For example, *Ornithosuchus*, the presumed ancestor of birds in Heilmann's

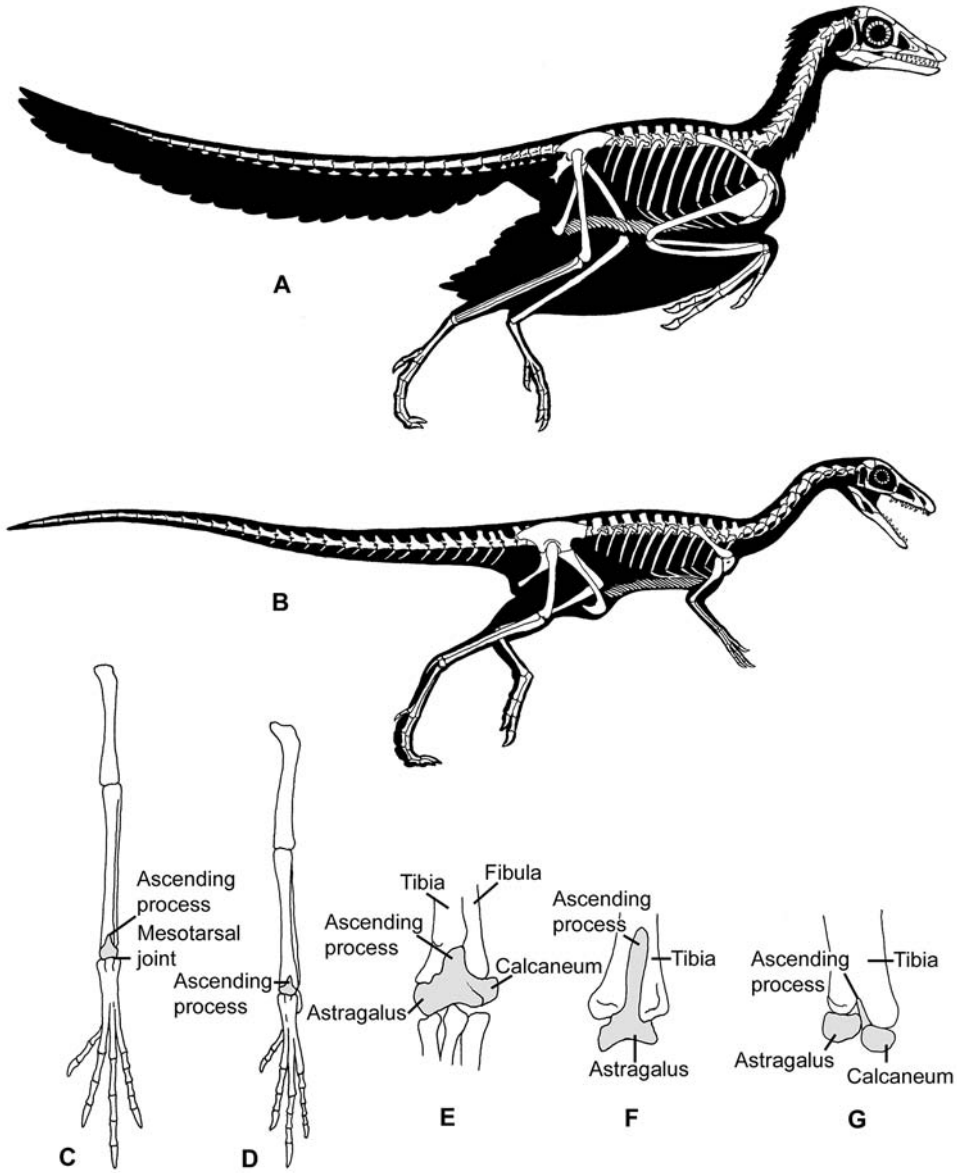


Figure 3.1. Close skeletal similarities such as bipedal posture and ankle structure between the early bird *Archaeopteryx* and the theropod dinosaur *Compsognathus*, both known from the Late Jurassic Solnhofen Limestone of Germany, led Thomas Huxley to propose that birds evolved from theropod dinosaurs in 1860s. A-B, comparison of the skeleton of *Archaeopteryx* with that of *Compsognathus*; C-D, comparison of the hindlimb of *Archaeopteryx* with that of *Compsognathus*; E-G, comparison of the ankle structure of the theropod *Allosaurus* (E), a juvenile ostrich (F), and an embryonic chicken (G) to show the ascending process on the astragalus and mesotarsal ankle joint.

schemata, is nested in Crurotarsi, which gave rise to the crocodilian lineage, entirely opposite to the avian line. Similarly, *Euparkeria*, another of Heilmann's favorite bird ancestors, is currently considered as an outgroup of archosaurs, a lower branch in the phylogenetic tree that is far removed from the avian lineage. Thus, the thecodontian hypothesis has become less attractive with the development of cladistic phylogeny, which better expresses the interrelationships of different clades.

Contrary to what Heilmann used as his central argument for rejecting the theropod hypothesis, clavicles are now known in many theropod dinosaurs. Because

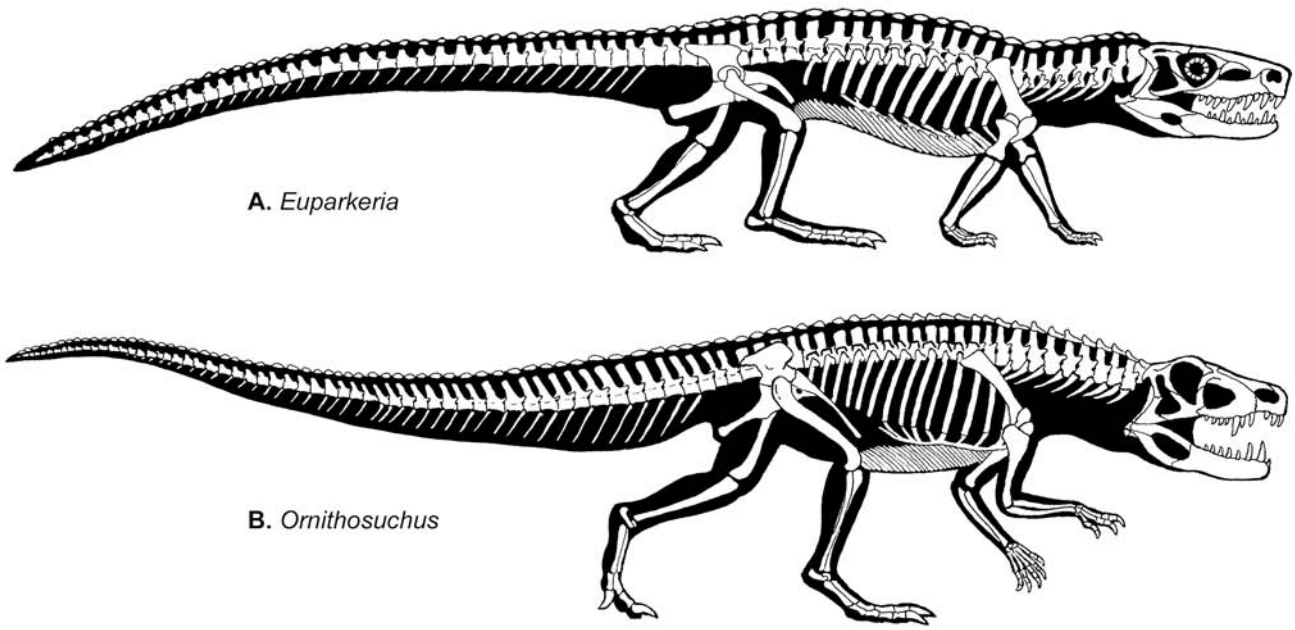


Figure 3.2. Gerhard Heilmann's (1926) thecodont origin of birds. Heilmann suggested that Triassic thecodonts such as *Euparkeria* (A) and *Ornithosuchus* (B) gave rise to early birds such as *Archaeopteryx*.

of its delicate structure and rib-like morphology, the collarbone had gone unrecognized in theropods for a long time. Thus the stumbling block for the theropod-bird link in Heilmann's argument has been removed with the discovery of clavicles in several groups of theropods.

In the early 1970s, John Ostrom of Yale University revived Huxley's theropod origin of birds, and suggested that small maniraptoran theropods, such as dromaeosaurs, come very close indeed to the ancestry of *Archaeopteryx* (Ostrom 1976a). For example, he showed the unique swivel wrist joint shared by the dromaeosaurid *Deinonychus* and *Archaeopteryx* that allowed the movement of the hand in the plane of the forearm but restricted movement in other directions (fig. 3.3). In addition to the swivel wrist joint, Ostrom presented an impressive array of skeletal similarities between dromaeosaurs and *Archaeopteryx*, such as hollow bones; a strap-like scapula; a long coracoid; long arms equipped with three fingers and sharp claws; a backwardly directed pubis; long, slender hind legs; three-toed feet; and a stiff tail. The striking resemblance between dromaeosaurs and *Archaeopteryx* must reflect a close evolutionary relationship, not convergence, Ostrom argued.

However, Ostrom did not accept birds as living dinosaurs. Subsequent cladistic analyses provided the empirical evidence that birds are descended from dromaeosaur-like theropods, called maniraptorans, which share with birds characteristic half-moon-shaped wrist bones, allowing the hand to be flexed sideways toward the forearm; this swivel wrist joint is responsible for the wing-folding mechanism in birds (Ostrom 1976a; Gauthier 1986). Application of cladistic phylogeny to dinosaurian taxa, beginning in the early 1980s, led to the large-scale pattern of theropod phylogeny and secured the position of birds within the maniraptoran theropods (Gauthier and Padian 1985; Gauthier 1986; Holtz 1994; Sereno, 1997; Makovicky and Zanno 2011). In this phylogenetic analysis, birds became maniraptoran theropods. Among maniraptorans, the early birds including *Archaeopteryx* and their descendants are now grouped in a clade called Avialae (Gauthier 1986).

A recent discovery from China indicates that maniraptoran fossils preserve complex, asymmetrical flight feathers like those of *Archaeopteryx* and *Jeholornis*, thus strengthening the evolutionary relationships between

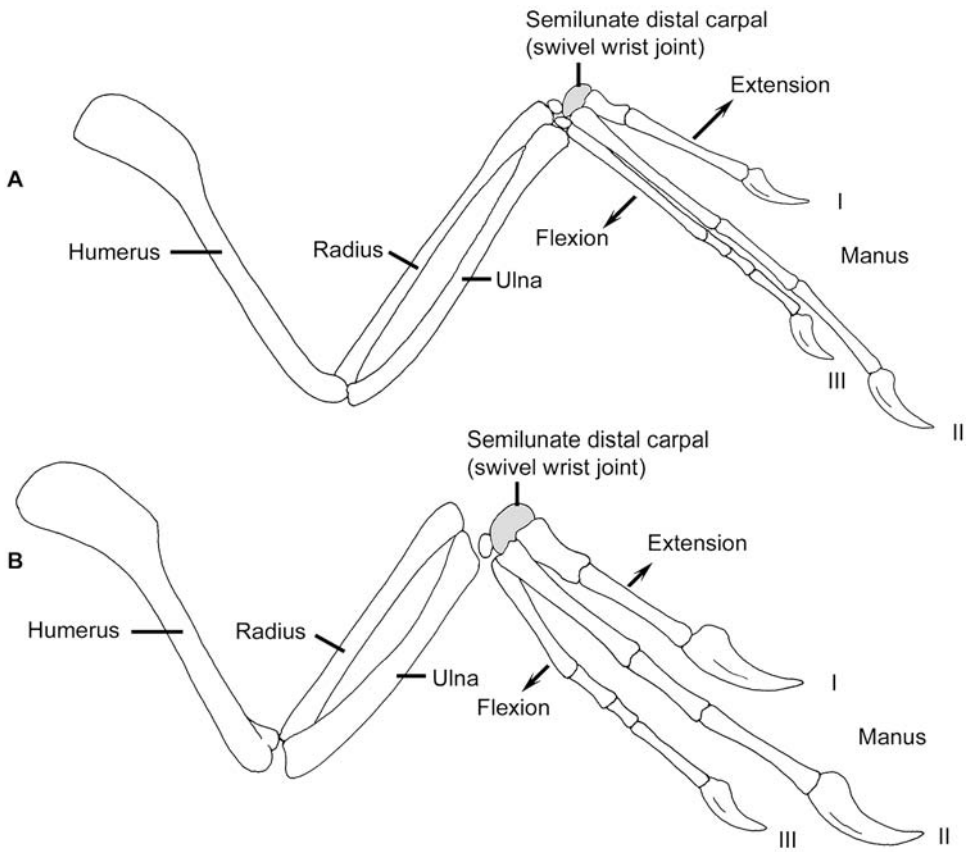


Figure 3.3. Close similarities of forelimb proportion and the wrist joint of the early bird *Archaeopteryx* (A) with that of dromaeosaurian theropod *Deinonychus* (B), showing a swivel wrist joint with the development of a semilunate distal carpal, led John Ostrom to revive the theropod hypothesis of the origin of birds in 1970s.

these maniraptorans and early birds (Xu et al. 2001, 2010). This new hypothesis that "birds are maniraptoran theropods" (the BMT hypothesis) has become widely accepted by both scientists and the general public, and will be discussed in detail in a later section in this chapter.

Avialan Origins from 1970 to the Present

Ostrom's idea of a theropod origin of birds and the BMT hypothesis came at a time of renewed interest in the ancestry of birds, when several alternative hypotheses involving other branches of archosaurs, or even basal diapsids, were proposed, which marked a revival of Heilmann's thecodontian proposal, far from the dinosaur line (Tarsitano and Hecht 1980; Welman 1995; Feduccia 1996, 2012; Czerkas and Yuan 2002; Czerkas et al. 2002; Martin 2004; Feduccia et al. 2005, 2007; Walker 1972, 1974, 1977; Martin 1985, 1991). Like Heilmann's idea, the general theme of this view is that birds and dinosaurs might have shared a common ancestry (early archosaurs), but dinosaurs did not give rise to birds because of a temporal paradox (the conflict in timing of the appearance of theropod ancestors and avian descendants in the stratigraphic record).

The Temporal Paradox

The proponents of the nontheropod hypothesis find temporal inconsistencies in trying to maintain that birds evolved from ancestors that lived many millions of years after the origin of birds took place. This apparent discrepancy between stratigraphy and phylogeny has been widely used to argue against the theropod hypothesis. For example, Ostrom derived the Late Jurassic (150 mil-

lion years old) *Archaeopteryx* from the Early Cretaceous (95 million years old) *Deinonychus*, as pointed out by the critics of the theropod hypothesis (Martin 1983b; Feduccia 1996, 2012); the anatomical similarities between dinosaurs and birds, according to them, are due to evolutionary convergences. However, the objections of the temporal paradox are unfounded because proponents of the theropod hypothesis point out that maniraptorans such as *Deinonychus* or *Velociraptor* shared with *Archaeopteryx* an unknown common ancestor that lived possibly in the Middle or even Early Jurassic time, as opposed to being direct ancestors of birds (fig. 3.4A). None of the Cretaceous maniraptorans are truly regarded as direct ancestors of birds. The application of cladistic relationships and the discovery of a near-bird fossil such as *Anchiornis* from the Middle-Late Jurassic of China resolve the temporal paradox issue of bird origins (fig. 3.4B).

Because of the temporal paradox, the critics of the theropod hypothesis proposed new alternative views, "nontheropod origins" (NTO) of birds (James and Pourtless 2009), which are briefly discussed here in a phylogenetic context to assess their merits. These putative reptilian ancestors in the NTO hypothesis are poorly preserved Triassic forms, which are distantly related to early birds because they share primitive reptilian body plans. They are so generalized and primitive that an avian body plan could be derived from these putative ancestors by multilevel acquisition of avian characters. In contrast, a theropod origin requires only a few steps to acquire bird characters and is a simpler and more parsimonious explanation because theropods had already developed a large suite of avian characters related to flight and locomotion. Parsimony, the simplest scientific assumption in the formulation of a theory that fits the evidence, is the guiding principle in choosing among alternate genealogies in phylogenetic analysis. It requires the fewest evolutionary changes to build a phylogenetic tree and derive birds from theropods.

Most of the avian characters cited by the nontheropod hypotheses are spurious and cannot be verified independently. They are hampered by plesiomorphic diagnoses or overreliance on particular typological morphologies

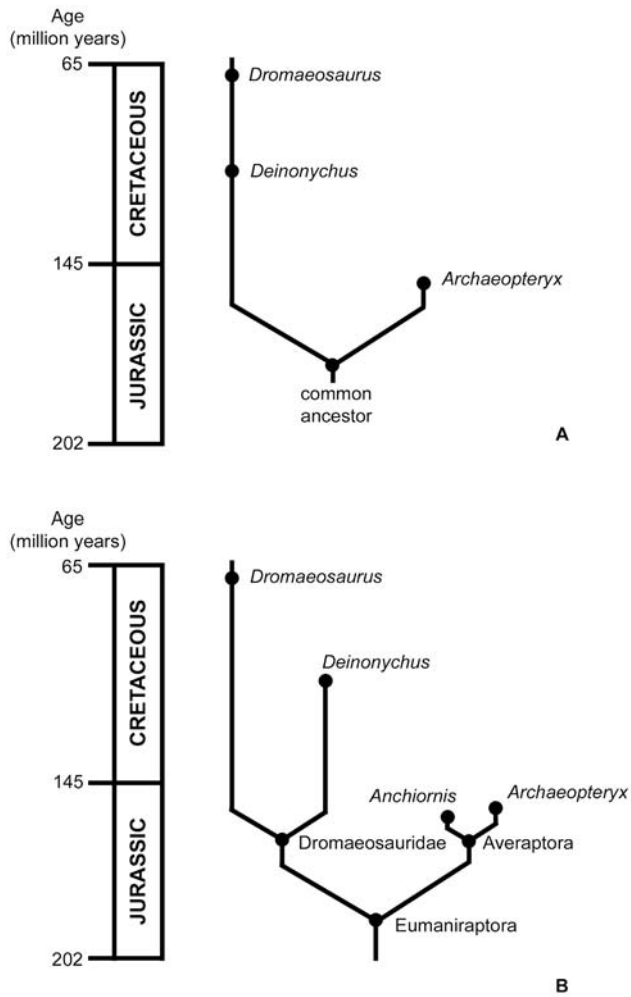


Figure 3.4. A, the apparent discrepancy between stratigraphy and phylogeny, called "temporal paradox," has been used to argue against the theropod hypothesis. The Cretaceous maniraptoran theropods such as *Deinonychus* and *Dromaeosaurus*, which are generally considered the closest relatives to the Late Jurassic birds such as *Archaeopteryx*, have been found in post-*Archaeopteryx* sediments. The critics argue that nonavialan maniraptorans such as *Deinonychus* and *Dromaeosaurus* lived millions of years after *Archaeopteryx*, thus they cannot be the ancestors of birds. This temporal paradox argument is somewhat flawed because the theropod hypothesis suggests that *Deinonychus* and *Dromaeosaurus* shared a common ancestor with *Archaeopteryx* as opposed to being direct ancestors of birds. Differential preservation of the fossil records of two closely related lineages creates this paradox. B, the application of cladistic relationships and the discovery of near-bird fossils such as *Anchiornis* from the Middle-Late Jurassic of China solve the temporal paradox issue.

such as small body size. This results in an oversimplified but ambiguous taxonomy and rampant paraphyly. Many of these fossils are fragmentary and their interpretations of avian affinity are dubious. The temporal sequence of ancestor-descendant relationship was the prime factor in selecting such a wide range of Triassic reptiles that existed before *Archaeopteryx*. Stratigraphy was the guiding principle of the NTO hypothesis; close anatomical similarities were considered secondary or irrelevant to the question of the ancestry of birds.

The Ankle Joint and the Phylogeny of Archosaurs

Birds are traditionally considered archosaurs because of three shared features in the skull: an antorbital fenestra between the external naris and orbit, the ossified laterosphenoid in the braincase, and the mandibular fenestra in the lateral side of the lower jaw. To understand how birds are related to a specific group of archosaurs, we need to examine the phylogeny of archosaurs. Recent cladistic analyses recognized two distinct lineages of archosaurs (fig. 3.5A), one leading to crocodilians (Crurotarsi) and the other to birds (Ornithodira) (Gauthier 1986; Sereno 1991). The key character for the basal dichotomy of archosaurs seems to be the different style of ankle joint. The Crurotarsi includes phytosaurs, ornithosuchids, aetosaurs, rauisuchians, and crocodylomorphs, all of which have a crurotarsal ankle joint. In this group the astragalus and calcaneum articulate with each other by means of a peg-and-socket joint, allowing rotational movement between them. Functionally, the astragalus is part of the crus and the calcaneum is part of the pes (fig. 3.5B). The calcaneum is very large and bears a prominent heel, or tuber, at the back for the attachment of the gastrocnemius muscle. The heel acts as a lever for raising the metatarsals during locomotion. In this group, the foot is primitively designed and pentadactyl like that of crocodilians, with a plantigrade pose so that the heel touches the ground (fig. 3.5C).

The Ornithodira includes pterosaurs, lagosuchids, silesaurids, ornithischians, sauropodomorphs, and theropods. In this assemblage, in the mesotarsal ankle a hinge joint is found between the proximal and distal rows of the tarsals. The calcaneum is highly reduced, lacks the heel, and is fused to the astragalus. Functionally, the astragalus and calcaneum are part of the crus, while the distal tarsals are part of the pes. The astragalus is a mediolaterally elongated hemicylinder with an ascending process for locking of the tibia, a feature first shown by Huxley (1870) to be unique to theropods and birds (fig. 3.5D). The mesotarsal ankle joint is associated with improved posture and a digitigrade pes, with the heel raised off the ground, and the middle three metatarsals form a tridactyl pes (fig. 3.5E). The shortened contact with the ground and the permanent elevation of the sole led to cursorial (running) locomotion. The mesotarsal ankle joint and the ascending process of the astragalus tie theropods to early birds.

Nontheropod Origins of Birds

Although the theropod origin of birds is now well accepted by the paleontologic community, several advocates also vigorously contested it from the perspective of evolutionary taxonomy, where the identification of an ancestor in a lineage is an important task. The critics argue that early birds such as the Late Jurassic *Archaeopteryx* must have evolved from Late Triassic ancestors, but their choice of ancestor has varied considerably across the phylogeny of nondinosaurian diapsid groups. In a cladistic framework, the putative ancestors range from a basal diapsid to an archosauromorph to an archosauriform to a crocodylomorph to an ornithodiran. Thus some of the nontheropod proponents not only deny a theropod origin, they also ignore the archosaur affiliation of birds, which is well secured by several shared derived characters. They choose the ancestors of birds from among some enigmatic, poorly known, nonarchosaur forms. The rationale for choosing these Triassic ancestors of birds was that they were small and quadrupedal reptiles with triangular skulls, small teeth, and a generalized body plan, and that they existed before the time of *Archaeopteryx*. The temporal sequence rather than anatomical similarity is the main argument in these views. However, these criteria do not constitute actual evidence relevant to the ancestry of birds. The anatomical evidence for choosing

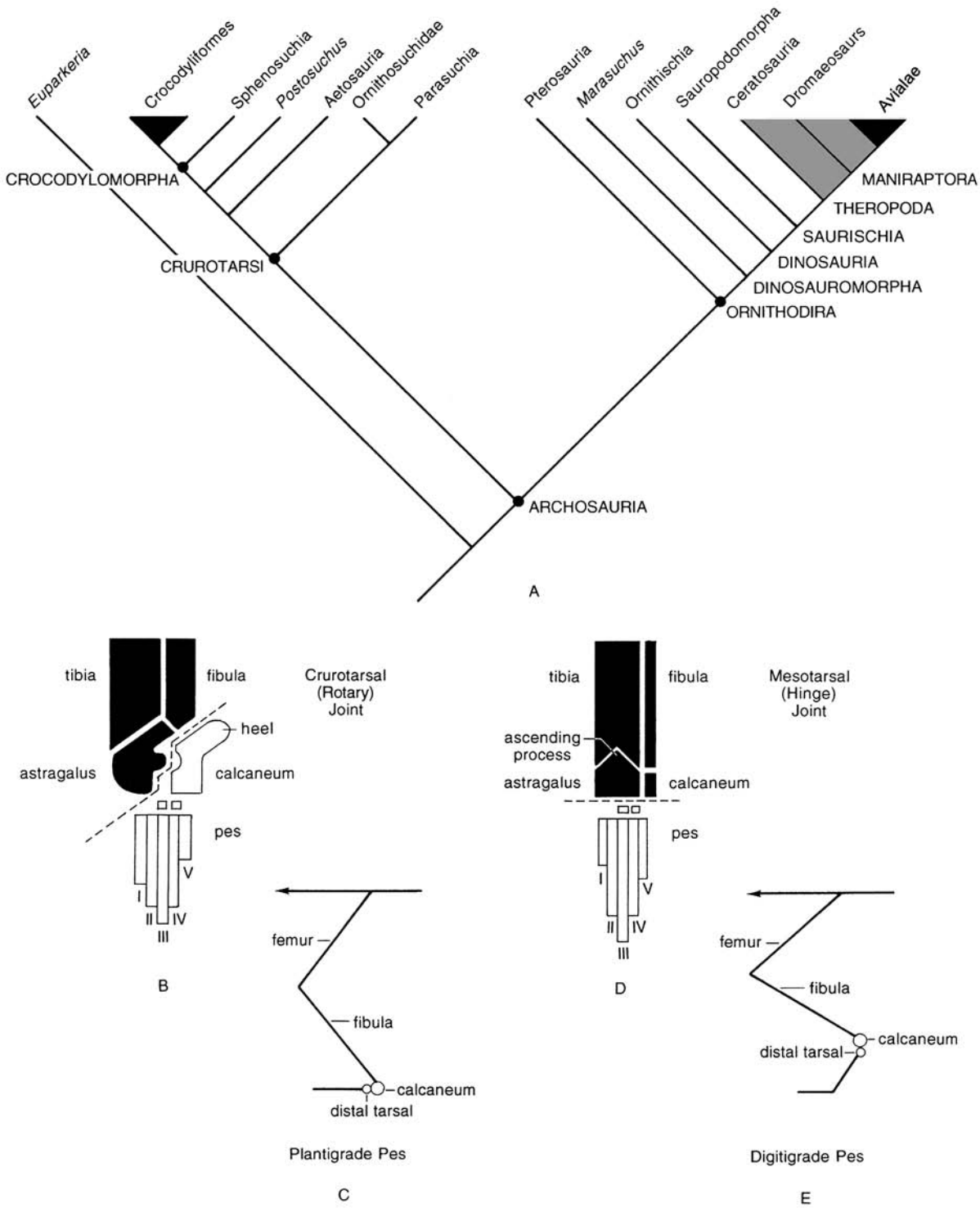


Figure 3.5. The phylogeny of archosaurs. A, cladogram showing the postulated relationships of the basal dichotomy of archosaurs into Crurotarsi (leading to crocodilians) and Ornithodira (leading to birds) (Chatterjee 1997). B, the crurotarsal ankle joint, in which the astragalus forms part of the crus, but the calcaneum, distal tarsals, and combined metatarsals move as a unit on the astragalus and fibula. The peg-and-socket joint between the astragalus and the calcaneum allows rotary motion between them. C, schematic lateral view of the hindlimb of the Crurotarsi showing the primitive, plantigrade pose. D, the characteristic hinge joint of Ornithodira between the proximal and distal rows of the tarsi. The astragalus and calcaneum are fused and form functionally as part of the crus. The astragalus has a typical ascending process for locking the tibia; the calcaneum is reduced. E, schematic lateral view of the hindlimb of the Ornithodira showing improved posture and the digitigrade pes.

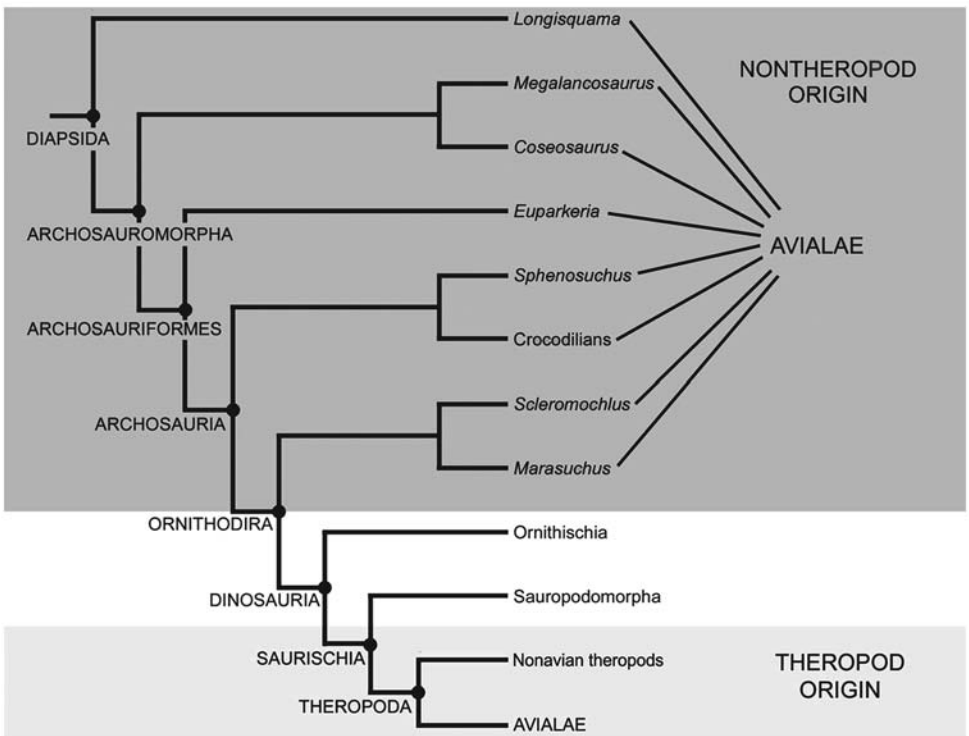


Figure 3.6. A cladogram showing several nontheropod origins (NTO) of birds from different branches of Triassic diapsid reptiles. Most of these potential ancestors are poorly preserved and show very few avialan attributes.

these poorly preserved ancestors is weak at best, a default option that was probably motivated by "an argument of opposition rather than an argument of advocacy" just to refute theropod origin (Witmer 2002, 17).

Here I discuss briefly five major hypotheses for the origin of birds from nontheropod ancestors as alternatives to the BMT hypothesis in a phylogenetic context (fig. 3.6). The putative ancestors of *Archaeopteryx* are:

1. early diapsid *Longisquama*
2. archosauromorphs such as *Cosesaurus* and *Megalancosaurus*
3. archosauriform *Euparkeria*
4. crurotarsan crocodylomorph archosaurs such as *Sphenosuchus* and *Dibothrosuchus*
5. ornithodiran archosaurs such as *Marasuchus* and *Scleromochlus*

These putative ancestral forms do not constitute a clade but represent a random pick from a wide range of small reptiles across the phylogeny of nontheropod diapsids at different hierarchical levels. Unfortunately, nontheropod origins of birds have never been explicitly formulated in a phylogenetic framework so that the shared characters cited by these authors could be assessed (Padian and Chiappe 1998; Dingus and Rowe 1998; Witmer 2002; Chiappe 2007; Sumida and Brochu 2000; James and Pourtless 2009).

Diapsid Origin

Longisquama is a small, enigmatic lizard-like reptile known from a poorly preserved skeleton and several incomplete fossil impressions from the Late Triassic Madygen Formation of Kyrgyzstan (Sharov 1970). Two potentially bird-like features are the triangular skull with a large orbit and the U-shaped clavicle. Poor preservation makes it difficult to assess the affinity of this animal. The most remarkable feature of *Longisquama* is a series of eight or nine pairs of long scales that fan out from the back, probably for gliding or display (fig. 3.7A). Each long scale looks like a fern leaf with a central shaft from which small scales project

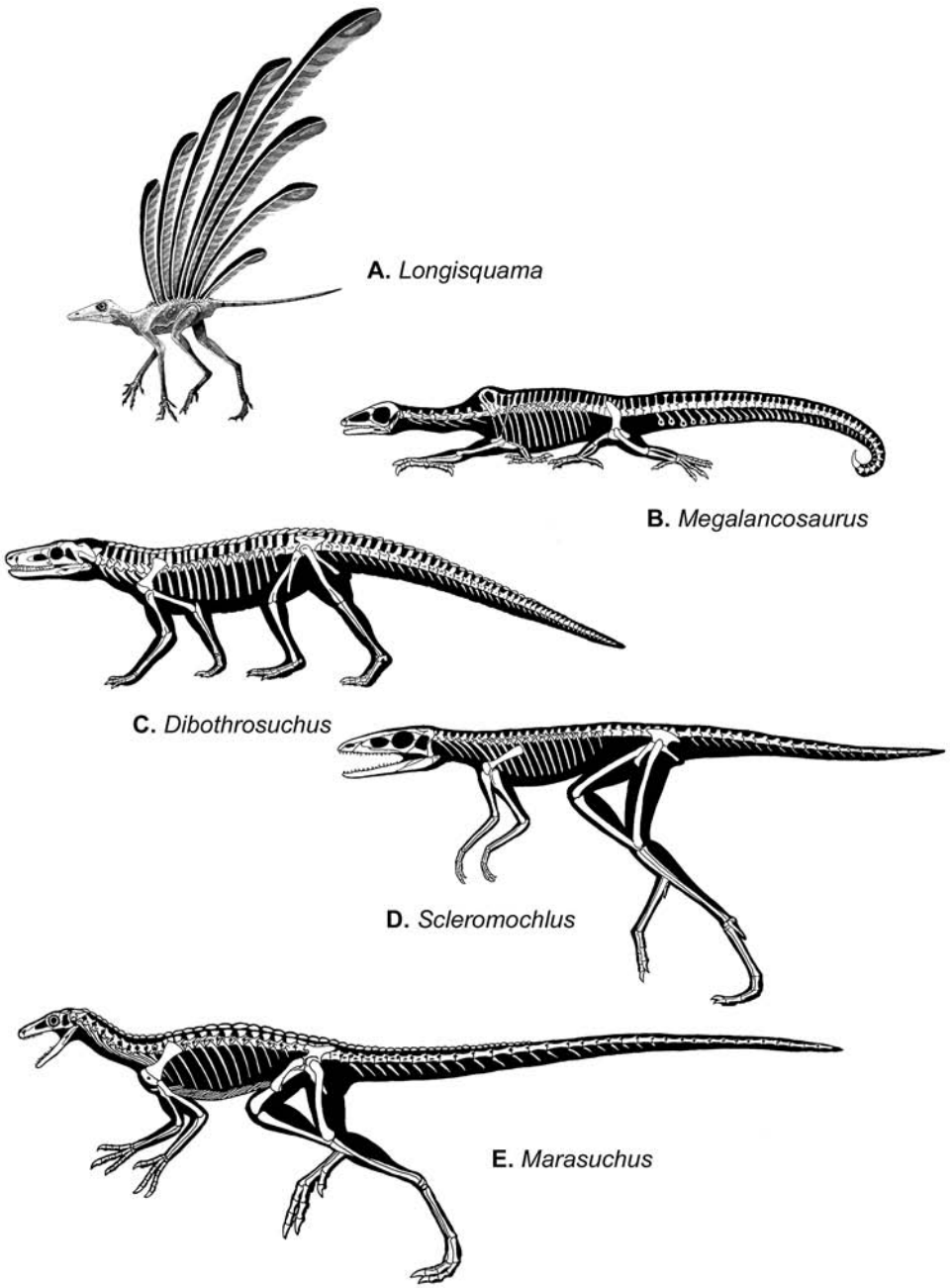


Figure 3.7. Several proposed candidates for nontheropod ancestors of birds; none shows unequivocal avian attributes. A, *Longisquama*, a small diapsid reptile from the Late Triassic of Kyrgyzstan with eight pairs of long scales for gliding; B, *Megalancosaurus*, a small, arboreal protorosaurid archosauromorph from the Late Triassic of Italy with large orbits and grasping hands and feet; C, *Dibothrosuchus,* a terrestrial crocodylomorph from the Early Jurassic of China; D, *Scleromochlus*, a bipedal ornithodiran archosaur from the Late Triassic of Scotland; E, *Marasuchus*, another bipedal ornithodiran archosaur from the Middle Triassic of Argentina.

perpendicularly like winglets of ancient insects. Haubold and Buffetaut (1987) interpreted these long fronds of scales as parachuting or gliding structures that could be folded and unfolded in butterfly fashion. Like wings in insects, the flight surface was not continuous but separated by gaps. Feduccia (2012) and Ruben and Jones (2000) have suggested that these structures are intermediate between scales and feathers, implying that *Longisquama* is closely related to the ancestry of birds. However, it appears from phylogeny (fig. 3.6) that *Longisquama* is deeply rooted in early diapsids, probably closely related to another gliding form such as the Permian *Coelurosaurovus*, and is farther removed from the origin of birds (Sumida and Brochu 2000). The scales of *Longisquama* were neither precursors to avian feathers, nor were they attached to the forelimbs. Gliding evolved convergently in many distantly related lineages of diapsids.

Archosauromorph Origin

Archosauromorphs include several stem groups of small assemblages of fossil diapsids and a very large group, the archosaurs, which includes familiar forms such as crocodiles, pterosaurs, dinosaurs, and birds (fig. 3.5). The basal groups of archosauromorphs from the Late Permian and Triassic include protorosaurs, rhynchosaurs, and trilophosaurs, which died out at the end of the Triassic. Among the basal archosauromorphs, several small protorosaurs (or prolacertians) such as *Megalancosaurus* and *Cosesaurus* have been cited as potential avian ancestors.

Megalanocosaurus, a small arboreal protorosaur (about 25 centimeters long) from the Late Triassic of Italy, has recently come into prominence as a potential avian ancestor (Renesto 2000). It had a large eye socket, grasping hands and feet with opposable digits, and a prehensile tail indicative of arboreal habits (fig. 3.7B). However, *Megalancosaurus* lacks the typical antorbital fenestra, a hallmark of archosaurs, including birds; its feet had opposable digits like those of a chameleon and the tail bears strange claw-like bony extensions that suggest the animal is too specialized to be linked to the ancestry of birds. It has an unusual shoulder girdle in which the scapula is rod-like with a spatulate base and the glenoid is a shallow socket between the scapula and coracoid; the sternal plates are large and conjoined to the large coracoids. The size and proportion of this animal and its large eye sockets might be linked to arboreal habits. None of the avian synapomorphies are present in the skeleton of *Megalancosaurus*.

Cosesaurus is a tiny, poorly known protorosaur fossil from the Middle Triassic of Spain, represented by a negative impression of the skeleton, with an elongate fifth toe, but the animal is difficult to interpret. Ellenberger (1977) proposed that *Cosesaurus* was an ancestor of modern birds. Its skull, large orbits, braincase, and beak-like jaws give a bird-like impression. Sanz and Lope-Martinez (1984) dismissed all of the avian traits of *Cosesaurus*, and relegated it to a juvenile *Macrocnemius*, a protorosaurian reptile known from Europe. Milner (1985) pointed out how progenetic dwarfism might have transformed a typical protorosaur skull of *Cosesaurus* into avian-like features.

Archosauriform Origin

The successive outgroups of archosaurs include several extinct Triassic forms such as proterosuchids, erythrosuchids, proterochamsids, and euparkeriids. The name Archosauriformes has been used to include these successive outgroups, plus Archosauria, which possessed the following synapomorphies: an antorbital fenestra (an additional hole in the snout wall between nostril and orbit), an ossified laterosphenoid bone in the braincase, lateral mandibular fenestrae in the posterior lower jaw bones, and laterally flattened teeth with serrations. Early archosauromorphs retained two temporal openings at the back of the skull, a quadrupedal gait, and the predatory habits of their diapsid ancestors. Among these groups, *Euparkeria*, a small facultative bipedal reptile from the Early Triassic of South Africa, probably an ancestor of all archosaurs, for which clavicles were known, would play a crucial role in the debate about the thecodontian origin of birds (fig. 3.2A) (Heilmann 1926).

Welman (1995) proposed the sister-group relationships between *Euparkeria* and *Archaeopteryx* on the basis of braincase morphology. However, Gower and Weber (1998) challenged this interpretation of the braincase

of *Euparkeria* as bird-like, but found close similarities to primitive archosaurs. *Euparkeria* is so primitive and generalized that it does not share any synapomorphies with birds (fig. 3.2A). Phylogenetic analysis suggests that *Euparkeria* lies outside the crown group of Archosauria (Sereno 1991).

Crurotarsan Origin

The archosaurs radiated into several groups during the Mesozoic and dominated the landscape. Although surviving archosaurs include only two lineages—the crocodiles and birds—far more spectacular in terms of body modifications and evolutionary radiations were several extinct groups such as pseudosuchians, pterosaurs, and dinosaurs during the Mesozoic. Among archosaurs, three putative ancestors of birds have been sought in crurotarsans (crocodylomorphs), basal ornithodirans, and theropod dinosaurs. The crocodylomorph origin is discussed first, followed by the ornithodiran and theropod hypotheses.

Alick Walker (1972, 1974, 1977) of the University of Newcastle-upon-Tyne, my former mentor, proposed a crocodylomorph origin of birds, a modified version of the thecodont hypothesis. He suggested that birds are more closely related to crocodiles than to other groups of archosaurs. He derived his hypothesis from *Sphenosuchus*, a primitive crocodylomorph from the Early Jurassic of South Africa that possessed many avian features in the skull, especially in the otic region. Some of these shared derived characters include a tympanic recess, a fenestra pseudorotunda, a bony Eustachian tube, elongated cochlear recesses, the loss of the descending process of the squamosal, and quadrate-prootic contact. Walker concluded that both crocodiles and birds were derived from a common ancestor among thecodontians. Wu and I described from the Early Jurassic of China a closely related sphenosuchian *Dibothrosuchus* (fig. 3.7C) that suggests that many of the putative avian characters in the crocodylomorph skull, especially pneumatic tympanic recesses that evolved convergently between the two groups (Wu and Chatterjee 1993). Larry Martin (1985, 1991) of the University of Kansas endorsed this crocodile-bird connection, supplemented by additional evidence from dental morphology and ankle structure. However, many of the synapomorphies of birds and crocodylomorphs proposed by Martin appear to be common to archosaurs (Gauthier 1986). Walker (1985) later rejected his own hypothesis and described these similarities between sphenosuchians and birds as superficial or convergent. The small brain size, primitive configuration of the brain, monimostylic quadrate, and akinetic nature of the skull of sphenosuchians provide the most serious argument against the crocodilian hypothesis. Many of the similarities shared by the crocodylomorphs and birds, especially in the ear region, are analogous, indicating similar functional requirements, perhaps associated with vocalization (Chatterjee 1991; Wu and Chatterjee 1993). Instead of evolving flight, early crocodylomorph history saw the beginning of a cursorial quadrupedal running style in the Late Triassic and Early Jurassic. The terrestrial lifestyle of early crocodylomorphs was followed by the adoption of a fully amphibious habitat from the Jurassic on, perhaps to avoid confrontation with dinosaurs, with the evolution of a thick, massive, akinetic skull, heavy body mass, a semierect quadrupedal gait, and dense bones, a body plan far from the featherweight and pneumatic design of the avian skeleton. With this dramatic ecological shift, crocodilians moved far away from the main line of bird evolution.

Ornithodiran Origin

Within the archosaurs, the sister lineage of crocodylomorphs is Ornithodira, which began to experiment with a lightweight skeleton, mesotarsal ankle joints, and bipedality to varying degrees. It is through the ornithodirans that we can trace two descendant lineages, the pterosaurs and dinosaurs. Two basal ornithodiran genera that have received attention as putative avian relatives are *Scleromochlus* from the Late Triassic Lossiemouth Formation of Scotland and *Marasuchus* from the Middle Triassic Chanares Formation of Argentina. *Scleromochlus* was a small archosaur, about 18 centimeters long, and has been often considered to be most closely related to, or ancestral to, Pterosauria (Sereno 1991). *Scleromochlus* (fig. 3.7D) is difficult to interpret because its tiny skel-

eton is preserved as natural molds of bones in a coarse sandstone matrix where many anatomical details are obscured. However, limb proportions and the gait of *Scleromochlus* may remove it from the putative ancestral position of birds. Its forelimb is slender but its hindlimb is much longer and more powerful than the forelimb, and the animal was a bipedal cursor with a digitigrade stance. The ankle is poorly known, but the calcaneum appears to have a heel as in crocodilians. In avian ancestry, we would expect the opposite trend in limb proportion, where the forelimb would be more elongated to evolve into a protowing; similarly, the ankle joint would be mesotarsal without any calcaneal heel. *Scleromochlus* shares no unique features with birds. If the ankle interpretation is correct, *Scleromochlus* is far removed from the ancestry of birds. Although Feduccia (1999) discounted an exclusive relationship between birds and *Scleromochlus* on the basis of limb disparity, he created a composite hypothetical ancestor of birds derived from it together with basal diapsids such as *Longisquama* and *Megalancosaurus*. Unfortunately, a sister-group relationship of birds cannot be established with a hypothetical hybrid derived from different lineages of diapsids and archosaurs.

Tarsitano and Hecht (1980) believe that *Archaeopteryx* could have evolved from a *Marasuchus*-like animal (fig. 3.7E). *Marasuchus*, a small, bipedal ornithodiran (about 40 centimeters long) from the Middle Jurassic of Argentina, shows some theropod-like proportions in the hindlimbs and has a mesotarsal ankle joint but does not share other synapomorphies with birds. Currently, *Marasuchus* is considered a sister group of dinosaurs and a distant relative of birds (Sereno and Arcucci 1993).

Theropod Origin of Birds

As discussed earlier, Thomas Huxley (1868b) first proposed the theropod-bird link on the basis of thirty-five shared characters. Huxley argued that Jurassic theropods such as *Compsognathus* show clear general skeletal affinities with *Archaeopteryx*, especially in the hindlimbs and girdles. John Ostrom (1976a, 1985a, 1991b) revived Huxley's theory of the relationship between theropods and birds and suggested that birds were the direct descendants of dromaeosaurs and shared a common ancestry. Huxley used the mesotarsal ankle joints as the key character, or synapomorphy, for uniting theropods with birds (fig. 3.1), whereas Ostrom recognized swivel wrist joints as the synapomorphy between dromaeosaurs and *Archaeopteryx* (fig. 3.3). However, Ostrom used traditional classification to separate dinosaurs and birds; he placed the birds in their own class, Aves, and dinosaurs in the class Reptilia, contrary to Huxley's grouping. However, his former student, Robert Bakker (1975), concluded that birds are actually theropod dinosaurs, not just descended from them. Like Huxley, Bakker argued that birds should not have their own separate class because they fly. Bats fly, too, but they are still considered mammals. Birds are as much dinosaurs as bats are mammals. Finally, Jacques Gauthier (1986) formalized the "birds are maniraptoran theropods" (BMT) hypothesis on the basis of detailed cladistic analysis that has enjoyed wide acceptance among paleontologists and evolutionary biologists.

To understand the bird's place in the dinosaur family tree, we must know the interrelationships of dinosaurs. Dinosaurs began their evolutionary history as small carnivores during the Late Triassic. They became diversified within a relatively short period of time and then ruled the earth for approximately 160 million years. During that time they adapted to a wide range of conditions and environments and became very successful. All known dinosaurs are divided into two major groups on the basis of pelvic structure—Saurischia and Ornithischia—and evolved into more than 1,200 different species during the Mesozoic. The Saurischia contains two subgroups: the plant-eating, mostly quadrupedal sauropodomorphs and the carnivorous, bipedal theropods. The Ornithischia includes several subgroups of herbivorous dinosaurs—armored thyreophorans (such as stegosaurs and ankylosaurs) and horned plus duck-billed cerapodans (such as ceratopsians and ornithopods). The theropods are the most spectacular of all dinosaurs and are linked to the ancestry of birds (fig. 3.8).

Gauthier (1986) provided the first detailed hypothesis of theropod relationships of birds on the basis of skeletal morphology; he recognized several monophyletic

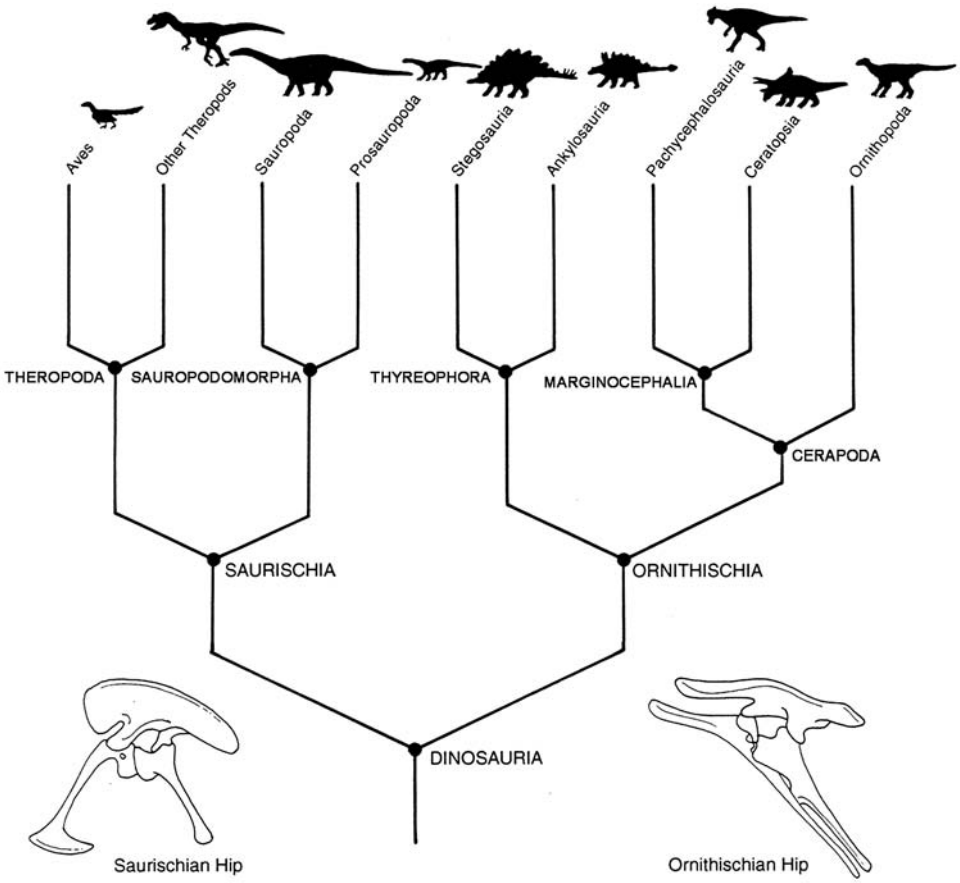


Figure 3.8. Cladogram showing how dinosaurs are related to each other—and how the birds fit in the dinosaur genealogy.

groups, or clades, in a hierarchical pattern. These successive clades are Theropoda, Tetanurae, Coelurosauria, Maniraptora, and Avialae (fig. 3.9). He showed that birds are actually maniraptoran theropods, the core concept of the BMT hypothesis. In fact, birds are now considered not only glorified theropods but also the sole surviving lineage of dinosaurs. The flying-dinosaur image of birds is appealing to the public and also is gaining currency among paleontologists (Weishampel et al. 2004; Sereno and Rao 1992; Chiappe 1995a, 2007; Chiappe and Witmer 2002; Chiappe 2007).

Ecological Partitioning in Theropods

Theropods remained habitual bipeds throughout their evolution, an antecedent body plan for avian stance and gait. Predatory adaptations that arose in the earliest terrestrial theropods include a flexible mandibular joint, sharp and compressed teeth, a long and powerful hand with recurved claws modified for grasping and raking, and a dynamic balancing tail stiffened by overlapping processes of prezyagapophyses (Ostrom 1976a). Theropods would revert to herbivory with loss of teeth several times in their evolutionary history. They would adapt a climbing and arboreal lifestyle with miniaturization of body size to evade predation, which would be a crucial stage in the evolution of early birds (Chatterjee and Templin 2004a, 2012). Tree-dwelling habits would encourage herbivorous or insectivorous adaptations in early birds.

For a long time, the transition from theropods to early birds has been documented by such a limited number of fossils that its early history remains obscure. The recent discovery of a wealth of spectacular fossils of early birds

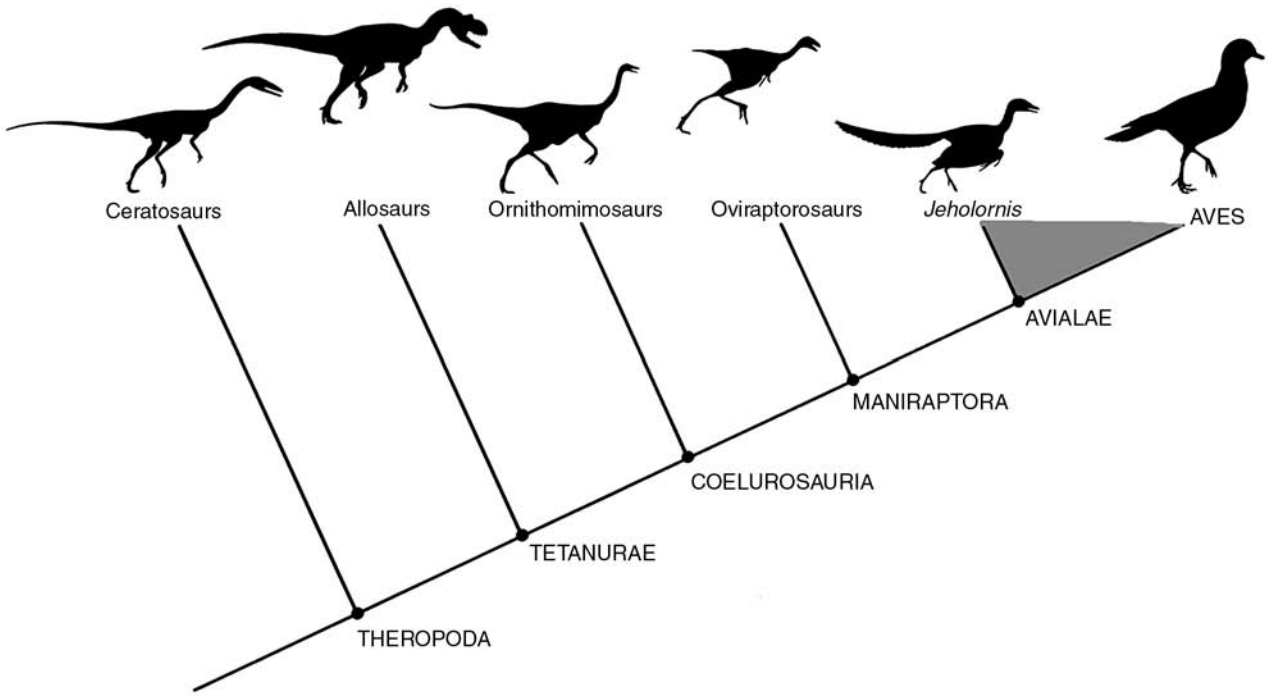


Figure 3.9. Simplified cladogram of theropod dinosaurs leading to birds. Birds (avialans) are deeply embedded within theropods, thus supporting the hypothesis that "birds are maniraptoran theropods" (BMT) (modified from Chatterjee 1997).

and their most immediate predecessors of feathered coelurosaurs from the Middle-Late Jurassic and Early Cretaceous of China and their arboreal lifestyle appears to have settled the century-old controversy of the origin of birds and their flight (see chapter 12).

All extant vertebrates that are parachuters and gliders are exclusively arboreal. Most likely birds evolved from a group of arboreal maniraptoran theropods that had developed feathers and rudimentary flight. Recent evidence has highlighted the fact that many features that were previously thought to be exclusive avian attributes such as a lightweight skeleton, hollow bones, elongated forearms, laterally flexing wrists, a wishbone, a sternum, perching feet, flight muscles, endothermy, a large brain, flight feathers, and primitive flight have now been discovered in the immediate theropod predecessors of birds that lived in trees above the ground. Hidden in these fossils are the clues to how birds acquired feathers and how they perfected their flying abilities from their maniraptoran ancestors. The strong anatomical similarities between coelurosaurian theropods and early birds suggest that flight imposes strict limitations on the shape, size, and structure of flying animals for aerodynamic efficiency.

Many feathered coelurosaurs became arboreal as reflected by their small size, with weight ranging from 500 grams to 1 kilogram, and several scansorial adaptations (Chatterjee 1997; Chatterjee and Templin 2004a, 2012). Increase in brain size, lengthening of the forelimbs, and improvement of feathers and flight surfaces coupled with decrease in body size appear to be general trends in arboreal coelurosaurs. Predator avoidance and invasion of new ecospace might be the stimulus for the arboreal adaptation of small coelurosaurs. Thus, miniaturization of size preceded the avialan node and the origin of flight; it evolved in many taxa of arboreal coelurosaurs when primitive flight adaptations such as parachuting or gliding developed. Side by side, their terrestrial counterparts became large with body size increasing by two to three

orders of magnitude (Turner et al. 2007). Some terrestrial forms became secondarily flightless from their arboreal forms to become large as they began to live on the ground and use different foraging techniques. Throughout the Cretaceous there were several events of secondary loss of rudimentary flight among coelurosaurs and concomitant gigantism.

Paul (2002) suggested that the most bird-like dinosaurs such as maniraptorans share bird-like features because they were secondarily flightless (or neoflightless). This may be partly true for large terrestrial coelurosaurs. Size could be used as a proxy to discriminate between arboreal and neoflightless forms. Thus the origin of birds from maniraptorans is a complex issue, complicated by two opposing forces: the refinement of flight in small arboreal forms and the loss of flight in large terrestrial forms; the latter became successful stealth predators. Tetrapterygids, the four-winged averaptors such as *Microraptor*, *Xiaotingia*, *Anchiornis*, and *Aurorornis*, which are now considered the close sister group of Avialae, were small, chicken-sized animals (fig. 3.10). During the early evolution of birds, we can look for small arboreal forms as potential avian antecedents across the theropod phylogeny. Once flight was perfected, avialans retained their small body size throughout the Cretaceous period.

Mapping the Theropod Heritage of Birds

The body plan of birds has been greatly influenced by their ancestry, method of feeding, reproduction, and dual mode of locomotion. Many of the features that we think are bird-like actually appeared in the nonavian theropod ancestors of birds. Since birds are theropods, we will use the recent theropod cladogram to trace the sequence of acquisition of avian characters in a phylogenetic context leading to *Archaeopteryx* and other avialans (fig. 3.10). Eight successive clades of theropods are reviewed here to trace the avialan ancestry: Theropoda, Tetanurae, Coelurosauria, Maniraptora, Paraves, Eumaniraptora, Averaptora, and Avialae. Although theropods are largely carnivores, herbivory may have evolved in some lineages of maniraptorans such as therizinosaurs and oviraptorosaurs.

If we look at the theropod cladogram (fig. 3.10), it becomes clear that birds should possess all of the characteristics of theropods, tetanurans, coelurosaurs, maniraptorans, paravians, eumaniraptorans, averaptorans, and avialans in a nested pattern (although some of them may have been lost or modified), but that they are also characterized by a suite of characters uniquely their own. In the phylogenetic scheme, birds are a derived group of theropods, which acquired many evolutionary novelties in the context of flight adaptation. The phylogeny of theropods provides a road map for understanding the acquisition of avian characters in each hierarchical level. The cladogram and character analysis represent a summary of recent studies on theropods by many workers (Gauthier 1986; Holtz 1994; Sereno 1997; Xu 1998; Xu et al. 2011; Makovicky and Zanno 2011; Turner et al. 2012; Godefroit et al. 2013a, 2013b; Agnolin and Novas 2013). Significantly, new fossil discoveries continuously update the genealogy of theropods.

Of all the dinosaurs, theropods are the most popular and intensively studied group that captures the imagination and generates much excitement because of our inherent fascination with predatory animals. Other than a fearsome skull equipped with sharp and recurved teeth, the trait that is probably most attributed to theropods in the public mind is the bipedal, cursorial adaptation that elevates its status to the top of the dinosaur food chain. Theropods represent the most successful group of dinosaurs; they alone survived the mass extinction at the end of the Cretaceous and radiated as modern birds. They are the only major clade of dinosaurs to retain the ancestral obligate bipedality throughout their entire history. As their descendants, birds acquired multimodal locomotion and exploited other ecospace such as air and water. In their skeletons, they retain unmistakable signs of theropod heritage. Let us review the successive clades of theropods to understand the gradual acquisition of avian characters in each hierarchical level.

Clades of Theropods

Theropoda

Theropods ("beast-footed"), like birds, were bipedal animals. All of them share several key features: a gracile body; slender, hollow, and pneumatic (air-filled) limb bones; a foot with three main toes; and a digitigrade stance. Most

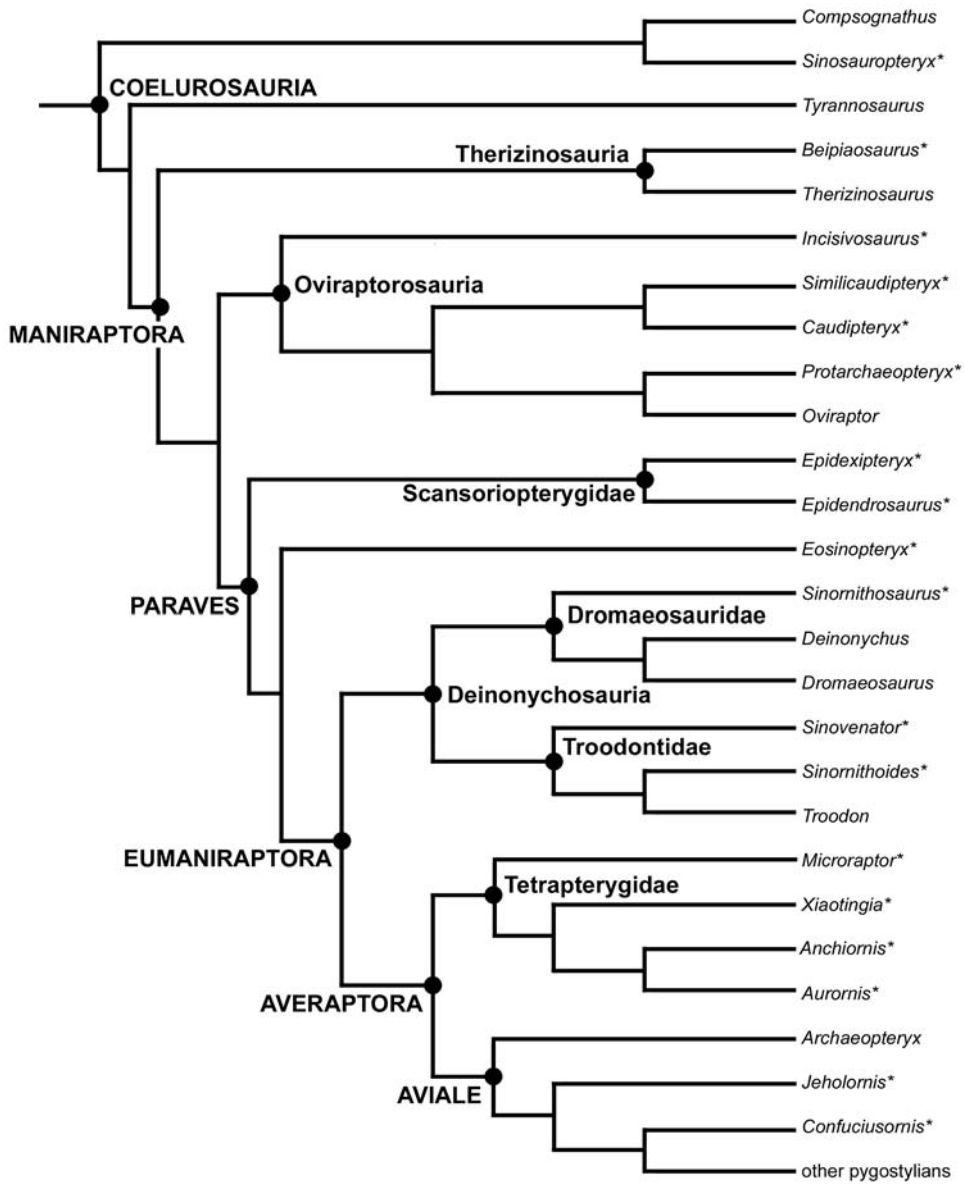


Figure 3.10. Generalized cladogram of feathered coelurosaurs from China showing the names of clades and genera employed in this book; the hierarchical relationships of the genera of feathered coelurosaurs and early avialans from the Daohugou and Jehol biota are noted with asterisks. This cladogram is followed throughout the text to trace the origin and early evolution of birds from theropod dinosaurs.

of the unique features of theropods are associated with their carnivorous habit and cursorial adaptation. They had powerful legs to run down prey; long grasping hands; and efficient jaws equipped with sharp, blade-like teeth for killing and slicing prey.

The skull is low and elongated and was attached to the neck at a highly mobile ball-and-socket joint that allowed rapid and precise movement of the head for catching prey. The orbits are large and frontally placed, indicating sizeable overlapping fields for distance judgment; apparently, theropods were highly sophisticated visual hunters. The lower jaw developed a kinetic or flexible joint between the anterior and posterior ramus, enabling it to spread laterally during the swallowing of prey. The forelimbs were considerably shorter than the hindlimbs and were not used for locomotion. The claws, especially on the

hand, were usually recurved and sharp for grasping and tearing flesh, and the mobile thumb worked with them in concert. The theropods were obligatory bipeds, where the long neck was cantilevered over the hindlimbs and the long tail counterbalanced the weight of the presacral region. The pelvis was very large and anchored with additional sacral vertebrae for strength and rigidity and provided considerable space for the attachment of powerful thigh muscles for locomotion. The outer two fingers began to lose their importance so that many later theropods retained only three inner fingers with a mobile thumb and elongated second and third fingers. In the foot, the first or big toe became reduced and separate from the pes, and the fifth digit was reduced to a splint, so the stance became tridactyl; the weight of the body would be borne by the three middle toes, II through IV (fig. 3.11). A recent spectacular discovery from the Middle-Late Jurassic and Early Cretaceous Liaoning Province of China suggests that feathers and their filamentary precursors possibly covered the bodies of most theropods for sexual display. The phylogeny of theropods documents how early birds evolved from predatory dinosaurs through several stages of evolutionary novelties.

Some of the earliest and most primitive theropods presently known from the Ischigualasto Formation of northwestern Argentina (about 227 million years ago) include *Eodromaeus* and *Herrerasaurus*. *Eoraptor*, long considered the most primitive theropod from the same formation, has been reclassified as a basal sauropodomorph. *Eodromaeus* was a small dinosaur about 1.2 meters long, with a lightly built skull fenestrated by several openings; the sympatric *Herrerasaurus* was longer, about 3 to 5 meters in total length. In *Herrerasaurus* a flexible intramandibular joint developed between the anterior and posterior parts of the lower jaw that enabled it to expand sideways during the gulping of large chunks of meat. The fourth finger was reduced and the fifth finger was lost in early theropods.

Among early theropods ceratosaurs represent the first widespread and diverse radiation spanning from Late Triassic to Late Cretaceous times. Early ceratosaurs such as *Coelophysis* are represented by hundreds of intact skeletons tangled together in a great jumble from the Late Triassic Chinle Group of Whitaker Quarry of Ghost Ranch in northern New Mexico, ranging in body length from 0.8 to 3 meters (fig. 3.11A). The general ceratosaurian features can be gleaned from the anatomy of *Coelophysis*. The skull is long, pointed, and lightly built, with sharp teeth lining the jaws. The orbits are large and face sideways. The lacrimal has a broad exposure on the skull roof. The quadrate head has moved considerably forward and fits into a separate squamosal socket without any paroccipital contact. There is an intramandibular joint between the dentary and postdentary bones. The quadratojugal is L-shaped. The palate is vaulted; the choana has been shifted backward so that the palatal processes of the maxilla form a false palate rostral to it. The two vomers are fused to meet the premaxillae. The brain is small (encephalization quotient [EQ] = 0.16) as revealed from the endocasts, and arranged in the reptilian fashion in tripartite division—the forebrain, the midbrain, and the hindbrain in which the optic lobes lie behind the cerebrum in the dorsal aspect (fig. 3.12). The otic capsule follows the basic archosaurian pattern, and shows two distinct foramina: the anterior one representing the fenestra ovalis for the stapes and the posterior one for the metotic foramina for cranial nerves IX-XI (fig. 3.13).

The postcranial skeleton is extremely lightly built; the limbs are long and slender, and the bones are hollow. The special posture and gait of birds—obligate bipedality—has already developed in this stage (fig. 3.11A). The long, lightweight skeleton is cantilevered over the powerful hindlimbs. The neck is longer than the trunk, and the sacrum is strengthened with five pairs of sacral ribs that are fused to the vertebrae and the ilia to form a rigid structure. The pectoral girdle contains fused clavicles, or the furcula. The ilium has a low, convex dorsal border and a long preacetabular process. The ischium and pubis are elongate and rod-like. The acetabulum is fully perforated, deep, and cylindrical, with a strong roof to resist the thrust from the head of the femur. The femur and tibia are strong bones. The tibia is 20% longer than the femur, indicating cursorial adaptation; the fibula is relatively slender and is closely attached to the tibia at the cnemial crest. The astragalus and calcaneum are fused to form a simple hinge with the mesotarsal joint. The astragalus has an ascending process that fits into the lower

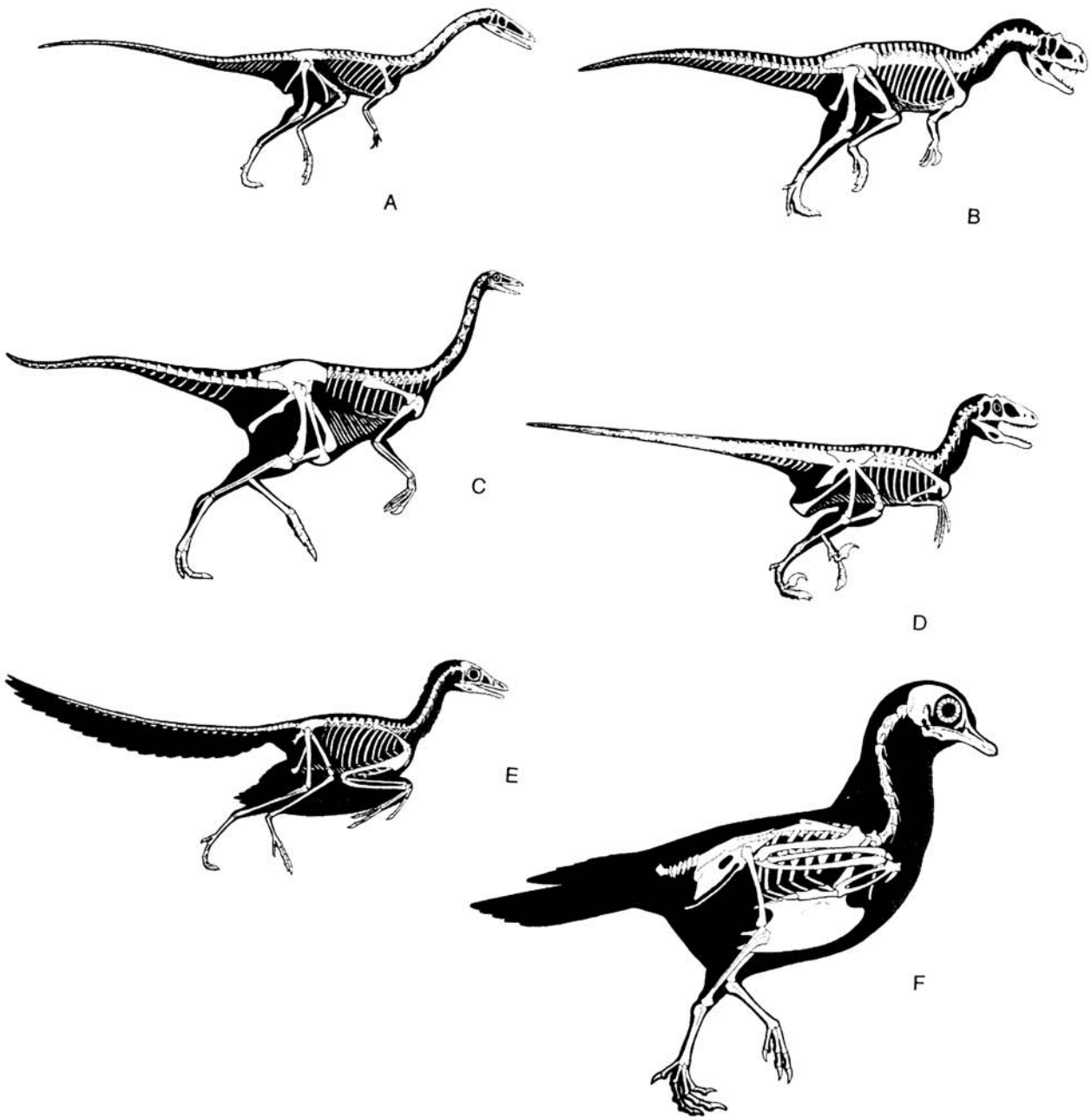


Figure 3.11. Some well-known theropods representing major clades leading to birds. A, *Coelophysis*, a ceratosaur from the Late Triassic of New Mexico; B, *Allosaurus*, a tetanuran from the Late Jurassic of Utah; C, *Ornithomimus*, a toothless coelurosaurian from the Late Cretaceous of North America; D, *Velociraptor*, a maniraptoran dromaeosaur from the Late Cretaceous of Mongolia; E, *Archaeopteryx*, a basal avialan from the Late Jurassic of Germany; F, *Columba* (pigeon), a modern bird. Bipedalism and erect posture are characteristics of theropods. There is a progressive change in the forelimb and shoulder girdle to form the flight apparatus. In nonavialan theropods, the tail is fairly long and the caudal vertebral count ranges from forty to fifty. The long tail indicates that the caudofemoral muscle, the main femoral retractor, was powerful in these groups. Rotation of the femur at the acetabulum (hip joint) was the primary mechanism of hindlimb locomotion. In dromaeosaurs, the tail was further strengthened with the development of ossified tendons to form a stiff, dynamic stabilizer (Ostrom 1979). In *Archaeopteryx*, the tail is truncated considerably and shows twenty to twenty-three vertebrae; truncation of the tail may be linked to reduction of the caudofemoral musculature (Gatesy 1990) so that the primary mechanism of hindlimb locomotion shifted from the hip joint to the knee joint. In later birds (*Columba*), the tail is further reduced to fewer than fifteen vertebrae with the development of a pygostyle; the tail is completely decoupled from hindlimb locomotion (after Chatterjee 1997).

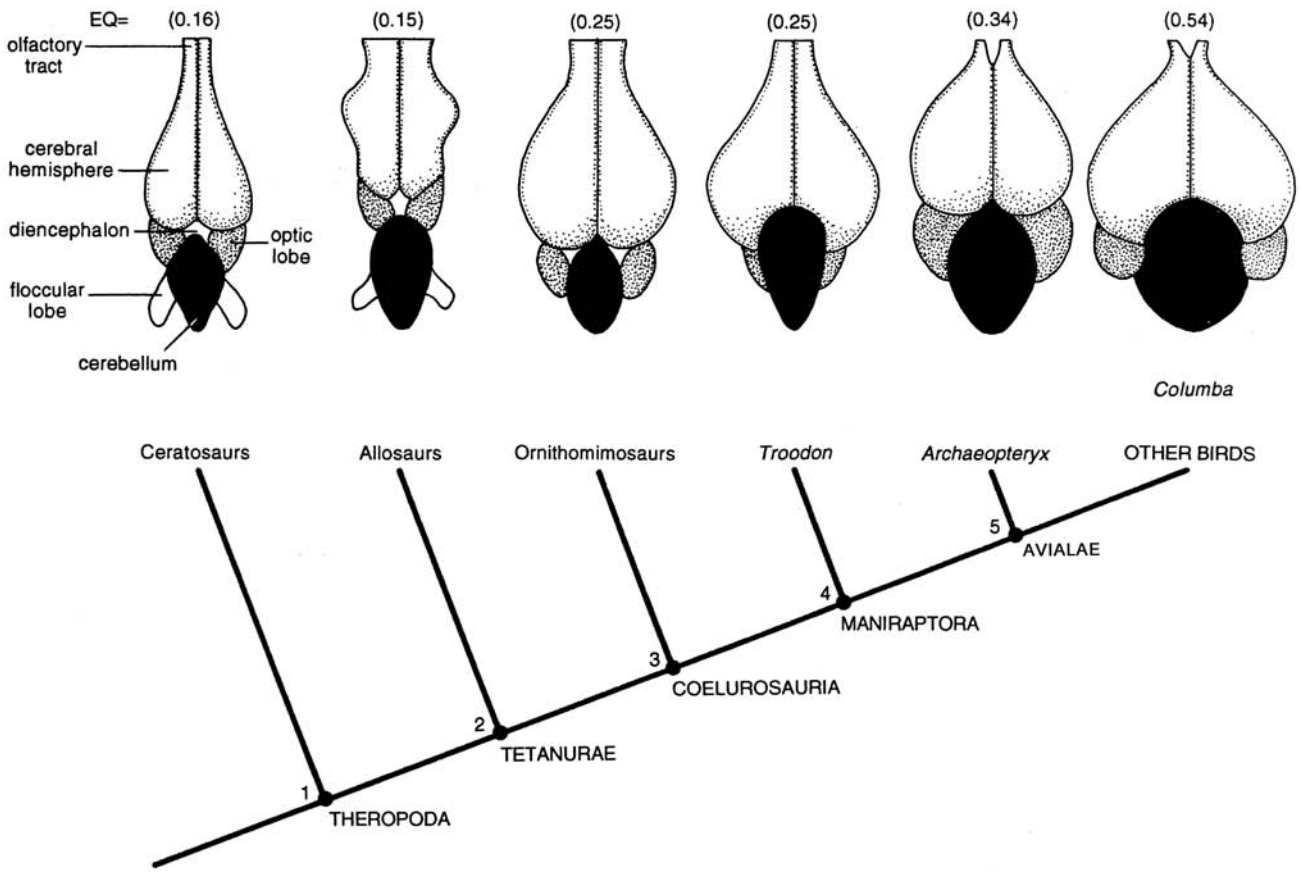


Figure 3.12. Diagrammatic dorsal views of the brains of major groups of theropods depicting the evolution of the avian condition in a cladistic relationship. There is a progressive increase in the encephalization quotient (EQ) from 0.16 to 0.54 as the brain becomes more and more enlarged. The EQ is generally high in predatory birds; it is 1.6 in crows (*Corvus*) (Chatterjee 1991). In terrestrial ceratosaurs (*Syntarsus*) and allosaurs (*Allosaurus*), the brain was small and primitively designed, with optic lobes immediately behind the cerebral hemispheres. The size of the forebrain (cerebral hemisphere), which controls most of the sensorial perceptions, approximately doubled in arboreal coelurosaurs. In ornithomimosaurs (*Dromiceiomimus*), the brain was enlarged in the avian fashion, and the optic lobes were displaced laterally and somewhat ventrally. This trend toward progressive brain enlargement continued in maniraptorans (Troodon), *Archaeopteryx*, and later birds (*Columba*).

Both ceratosaurs and allosaurs were fully terrestrial animals, like modern dogs, and lived in a two-dimensional world. The sudden enlargement of the brain in coelurosaurs may indicate their capability in an arboreal habitat, living in a three-dimensional world like modern cats. In *Archaeopteryx* and later birds (*Columba*), the cerebellum becomes progressively enlarged for balance and coordination, the optic lobes are enlarged for visual acuity, and the olfactory bulbs are highly reduced, indicating less dependence on smell. The brains of various nonavian theropods were made from endocasts (after Chatterjee 1997).

end of the tibia. The foot is exceedingly bird-like and digitigrade, with the middle three metatarsals complete and forming a tridactyl pes. The fifth metatarsal is reduced to a splint and lacks any digit. The first metacarpal is shortened, attached about halfway down metatarsal II; the pedal phalangeal formula is 2-3-4-5-0. Apparently, ceratosaurs were swift and agile runners with extremely long tails, reinforced by long, interlocking prezygapophyses.

Ceratosaurs split early into two lineages, the ceratosauroids and coelophysoids. Some of the ceratosauroids such as abelisaurs became the dominant predators in the Late Cretaceous ecosystems of Gondwana continents (South America, Madagascar, and India). One of the popular Argentinean abelisaurs, *Carnotaurus*, developed a robust, fearsome skull with paired horn-like structures above the eye sockets; a shallow, long neck; and extremely reduced forelimbs. Coelophysoids include small and lightly built forms such as *Coelophysis*, *Syntarsus*, *Dilophosaurus*, and

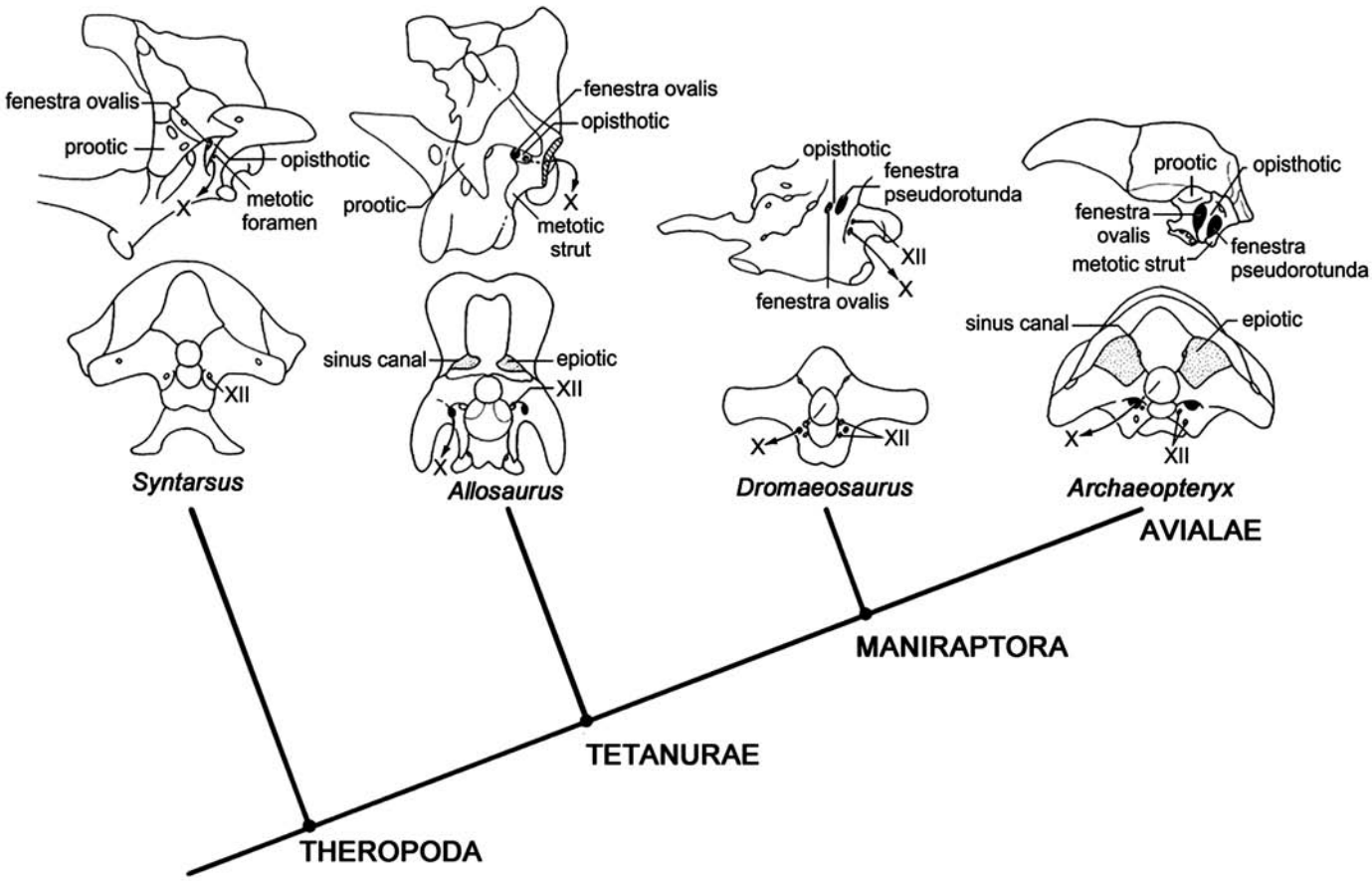


Figure 3.13. Diagrammatic lateral (*top*) and occipital (*bottom*) views of the braincase of major groups of theropods showing the evolution of the avian middle ear. In ceratosaurs (*Syntarsus*), the otic capsule is primitively built; it shows two large foramina on the lateral wall, separated by a stout bar of opisthotic. The rostral one is the fenestra ovalis, which receives the footplate of the stapes. The caudal one is the metotic foramen, which provides an exit for cranial nerves IX–XI and possibly the internal jugular vein. In allosaurs (Allosaurus) and ornithomimosaurs (*Struthiomimus*), a subscapular cartilage, the metotic strut, is added to the exoccipital, thus enclosing the rostral part of the metotic foramen. As a result, the vagus (X) foramen in these groups has been diverted backward from the metotic foramen behind the metotic strut and emerges at the occiput, lateral to the hypoglossal (XII) foramen. In Maniraptora (*Dromaeosaurus*), with the elongation of the cochlea, the perilymphatic duct is shifted to a new aperture, the fenestra pseudorotunda, at the position of the metotic foramen. The vagus foramen has severed its lateral connection through the metotic strut and takes a shorter route; it is now directed medially to the endocranial cavity. The opisthotic is further reduced in *Archaeopteryx* and later birds (*Columba*) and becomes largely internal to form a slender bar (after Chatterjee 1997).

Procompsognathus from the Late Triassic and Early Jurassic sediments.

Tetanurae

Tetanurans ("stiff tails") are more derived than ceratosaurs with the development of a delicate snout, a large ascending process on the astragalus in front of the tibia, stiffening of the posterior part of the tail, large hands with three fingers, and specialized wrists. The tetanurans are named for their stiff tails, which were less flexible than those of the ceratosaurs. The collarbones, or clavicles, are fused and extend between the two shoulder joints and the sternum to form the wishbone. Tetanurans are a large, diverse group of theropods and contain many popular forms such as *Allosaurus*, *Acrocanthosaurus*, and *Carcharodontosaurus*, as well as the crested genus *Cryolophosaurus* from Antarctica.

The most prolific tetanuran fossil record is represented by the mass accumulations of *Allosaurus* skeletons from the Morrison Formation of the Cleveland-Lloyd

Quarry of Utah. *Allosaurus* was a large theropod, about 12 meters long, with a massive skull on a short neck, a long tail, a reduced forelimb with three fingers terminating in sharp and recurved claws, and a powerful hindlimb (fig. 3.11B). The skull has a pair of pneumatic brow bridges, or horns, just above and in front of the eyes and the jaws are equipped with sharp, laterally compressed, and serrated teeth. The skull of *Allosaurus* and related groups shows several characteristics: the nasal participates in the formation of antorbital fossa; a flange-shaped lacrimal process occurs on the palatine; the basioccipital of the braincase is excluded from the basal tubera; and the articular of the lower jawbone has a strong medial process. In the skull, the teeth are lost at the back of the jaw so that the tooth row ends rostral to the orbit. The maxillary fenestra is developed within the antorbital fenestra. The lacrimal and jugal bones around the orbit are highly pneumatized. In the otic region, the beginning of the development of the metotic process can be seen. As a result, the vagus foramen has been diverted backward, tunneling through the metotic process and emerging at the occiput near the hypoglossal foramen (fig. 3.13). Recently, the vagus canal being posteriorly diverted to occiput has been identified in abelisaurs. At the occiput, there is a sinus canal that separates the supraoccipital from the epiotic. A tubular cochlear recess houses the lagena. The caudal tympanic recess is present at the front of the paroccipital process in some taxa. The quadrate has developed parastylic motion for mandibular spreading. The scapula is strap-like, whereas the posteroventral margin of the coracoid tapers. The hand is large, measuring half the length of the radius and humerus. It has three fingers; the fourth and fifth have been lost. Metacarpal I is very short; the manus phalangeal formula is 2-3-4-x-x. The ischium bears an obturator process; the pubis shows an expanded foot. The tibia has a wing-like anterior trochanter and transversely expanded distal end, whereas the astragalus shows a tall, broad, ascending process in front of the tibia. The pes is four-toed, with a reduced metatarsal I; the phalangeal formula is 2-3-4-5-x.

Coelurosauria

Among tetanurans, the coelurosaurs ("hollow-tailed") show several derived characters that lead to maniraptorans, paravians, eumaniraptorans, averaptorans, and finally avialans (early birds). Hence, coelurosaurs comprise all theropods that are closer to birds than to tetanurans. The coelurosaurian clade is distinguished from tetanurans on the basis of certain derived characters in the pelvis and foot morphology. For example, the ischium is reduced to two-thirds or less the length of the pubis, the ischial foot has been lost, and a triangular obturator process occurs on the ischium; the sacrum is extended (six sacral vertebrae), there is more extensive stiffening of the tail, the femoral fourth trochanter is reduced, and the ascending process of the astragalus is highly pronounced; in the foot the middle metatarsal bone becomes pinched, so that the other toe bones are closely appressed to form a strong and narrow tridactyl foot. Feathers have been found associated with many species of Chinese coelurosaurs of different shapes and sizes. The new evidence indicates that the mighty and fearsome *Tyrannosaurus rex* may have been covered with a coat of soft downy feathers. Many coelurosaurs became small and arboreal, and developed a variety of feathers. So far, sixteen genera of nonavian feathered coelurosaurs have been reported from the Daohugou and Jehol biota at different hierarchical levels that represent various stages of feather evolution leading to avialans (fig. 3.10). Many of these feathered coelurosaurs show extravagantly colored plumages, indicating that color vision developed in these arboreal forms for species recognition and sexual display. No doubt feathers evolved initially for insulation or sexual display before powered flight.

Among coelurosaurs the first lineage to consider is the Tyrannosauriadae, the gigantic, ferocious, and spectacular *Tyrannosaurus rex* and its close relatives. Although descended from small ancestors such as *Raptorex* (about 3 meters long), which is known from the basal member of the Jehol Group of China, tyrannosaurids were almost always the top predators in their respective ecosystems. As with most predators, emphasis is on the mouth as the

killing and feeding organ. Another small tyrannosaurid from the Jehol Group is *Dilong*, which had an insulative coat of feathers. Another sympatric feathered dinosaur from Liaoning is *Yutyrannosaursus*, which is gigantic and has a three-fingered manus; the body is covered long filamentous feathers. These basal Chinese tyrannosaurids were dwarfed by the king, *Tyrannosaurus rex*, which possessed all the attributes of the family such as a proportionately large skull, incisiform premaxillary teeth, diminutive forelimbs, a two-fingered manus, and powerful hindlimbs with cursorial proportions. Larger tyrannosaurs, as long as 7 meters, such as *Alectrosaurus* in China and Mongolia and *Eotyrannus* in the United Kingdom, appeared just a few million years later. Throughout the Late Cretaceous, tyrannosaurs diversified into several species, all with large skulls, powerful hindlimbs, and atrophied forelimbs with two fingers. The largest species was *Tyrannosaurus rex*, which was 13 meters in length and 7 tons in weight with a massive skull. The orbits are frontally placed with expansive stereoscopic vision that allowed the animal to judge how far away prey were. The endocast of the brain indicates enlarged olfactory and optic lobes. Thus, as in most predators both vision and smell must have been keen for detecting and capturing prey. The teeth are large, serrated blades arranged along curved jaws so that when the mouth is closed almost all the teeth can be engaged in capturing and killing prey. The skull was mobile and kinetic during feeding. The symphysis of the lower jaw between the two dentaries was loosely held by cartilage as in snakes, indicating some lateral movement at the tip during feeding. Side by side, the intramandibular joint between the anterior and posterior parts of the jaw ramus was highly flexible to allow the jaw joint to move outward when the mouth was closed to increase the diameter of the throat for swallowing large objects. The mandibular spreading continues in the avian lineage.

Another important group of coelurosaurs comprised medium to large, lightly built theropods, called ornithomimosaurs, which superficially resembled modern ostriches in size and proportion. Their delicate skulls with distinctive toothless jaws bordered by a bird-like beak indicate herbivorous adaptation, although some basal members retained a few teeth. The gastroliths found in the stomachs of some ornithomimosaurs suggest that these gizzard stones were used to grind vegetable food because these animals lacked grinding teeth. The ornithomimosaurs were lightly built with long cursorial hindlimbs and very long arms with slender hands (fig. 3.11C). They are mainly known from the Cretaceous beds of North America and Central Asia. Primitive members of this group include *Pelecanimimus* and *Harpymimus*, but more derived members are represented by *Struthiomimus* and *Ornithomimus*.

Sinosauropteryx was the first coelurosaurian from the Jehol biota, about the size of a rooster with a large skull, sharp teeth, short arms, and a long tail that got global attention in 1966 with the discovery of first evidence of feathers in nonavian theropods (Chen et al. 1998; Xu 2008). These hair-like downy feathers covered the body and tail of *Sinosauropteryx*. Recent detection of pigment-packed organelles, called melanosomes, in the feathers of *Sinosauropteryx* indicate orange-hued "protofeathers" in the body with thin dark stripes along the length of the tail (Zheng et al. 2010). These downy feathers could not have been used for flight, but probably served as insulation or for display.

Maniraptora

Among the coelurosaurs, maniraptorans ("hand grabbers") are a diverse assemblage made up of alvarezsaurids, therizinosaurs, oviraptorosaurs, deinonychosaurs, and avialans that evolved true broad contour feathers (fig. 3.14). The maniraptorans are distinguished from other coelurosaurs by an encephalized skull; elongated forelimbs; an ulna with a curved shaft; a semilunate carpal with a swivel wrist joint; a bony sternum; an ischium with a broad obturator notch and reduced distal symphysis; a backward-pointing pubis; and a stiff, dynamic tail, strengthened by ossified tendons. In the skull, the prefrontal is reduced. The otic region is considerably modified in avian fashion; a separate pseudorotunda can be seen behind the fenestra ovalis. The vagus foramen has severed its connection with the metotic foramen and takes a shorter route; it is now directed medially to the endocranial cavity (fig. 3.13).

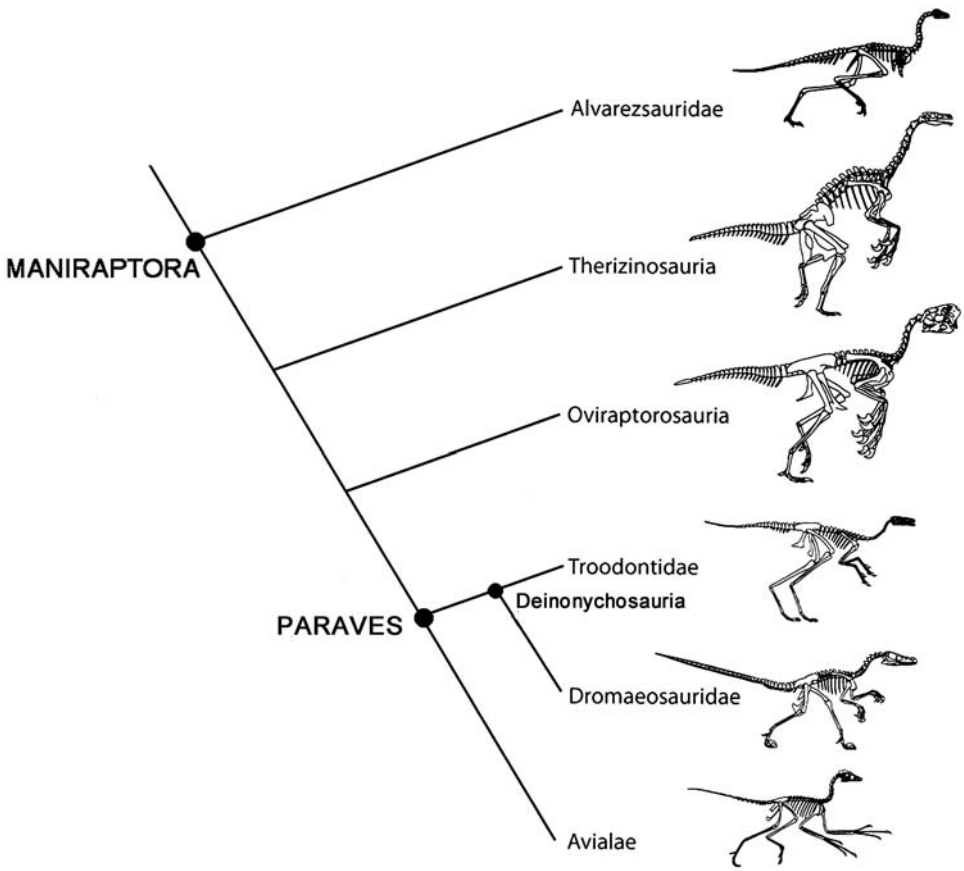


Figure 3.14. Cladogram showing interrelationships of major clades of maniraptorans with *Archaeopteryx* as a basal member of Avialae (after Turner et al. 2012). Recent phylogenetic analysis by Xu et al. (2011) placed *Archaeopteryx* as a member of the deinonychosaurs. To avoid the fluid phylogenetic position of *Archaeopteryx*, it is regarded as a member of the more inclusive clade Paraves.

The bony Eustachian tube is developed. The dorsal tympanic recess is formed at the lateral surface of the prootic. The coracoid is ventrally elongated, with a subtriangular profile. It has developed the biceps tubercle on the lateral surface of the coracoid. A semilunate carpal has provided a swivel wrist joint so that the hand can be folded tightly against the body in a Z fashion when not in use. The anterior process of the ilium is considerably enlarged and the pubis has rotated backward.

Some basal maniraptorans such as alvarezsaurids, therizinosaurs, and oviraptorosaurs were enigmatic groups of theropods with omnivorous or herbivorous adaptations and show various avialan traits. Alvarezsaurids had small beaky skulls with tiny teeth, powerful arms with huge thumb claws, and exceedingly small digits 2 and 3. Perle et al. (1993) reported a bizarre alvarezsaurid, *Mononykus olecranus*, from the Late Cretaceous of the Gobi Desert. As the name suggests, the animal had an atrophied forelimb with a prominent olecranon process on the ulna and a single claw (fig. 3.15A). It has been proposed that this turkey-sized animal had a tubular snout and elongated jaws, and dug holes with its shovel-like forefeet to prey on colonial insects such as termites. The jaws were probably edentulous except for minute teeth at the tips. A sympatric juvenile *Shuvuuia deserti* shows modified temporal configuration and the beginnings of skull kinesis as well as downy feathers covering the body (Chiappe 2007).

Oviraptorosaurs are a group of small Cretaceous maniraptorans, characterized by pneumatized boxy skulls, parrot-like beaks with a few teeth restricted to premaxilla or edentulous jaws, and short preorbital regions similar to those of basal avialans. Small basal oviraptorosaurs (body mass 500 grams to 1 kilogram) such as the toothy *Incisivorous*, *Caudipteryx*, and *Protarchaeopteryx* from the

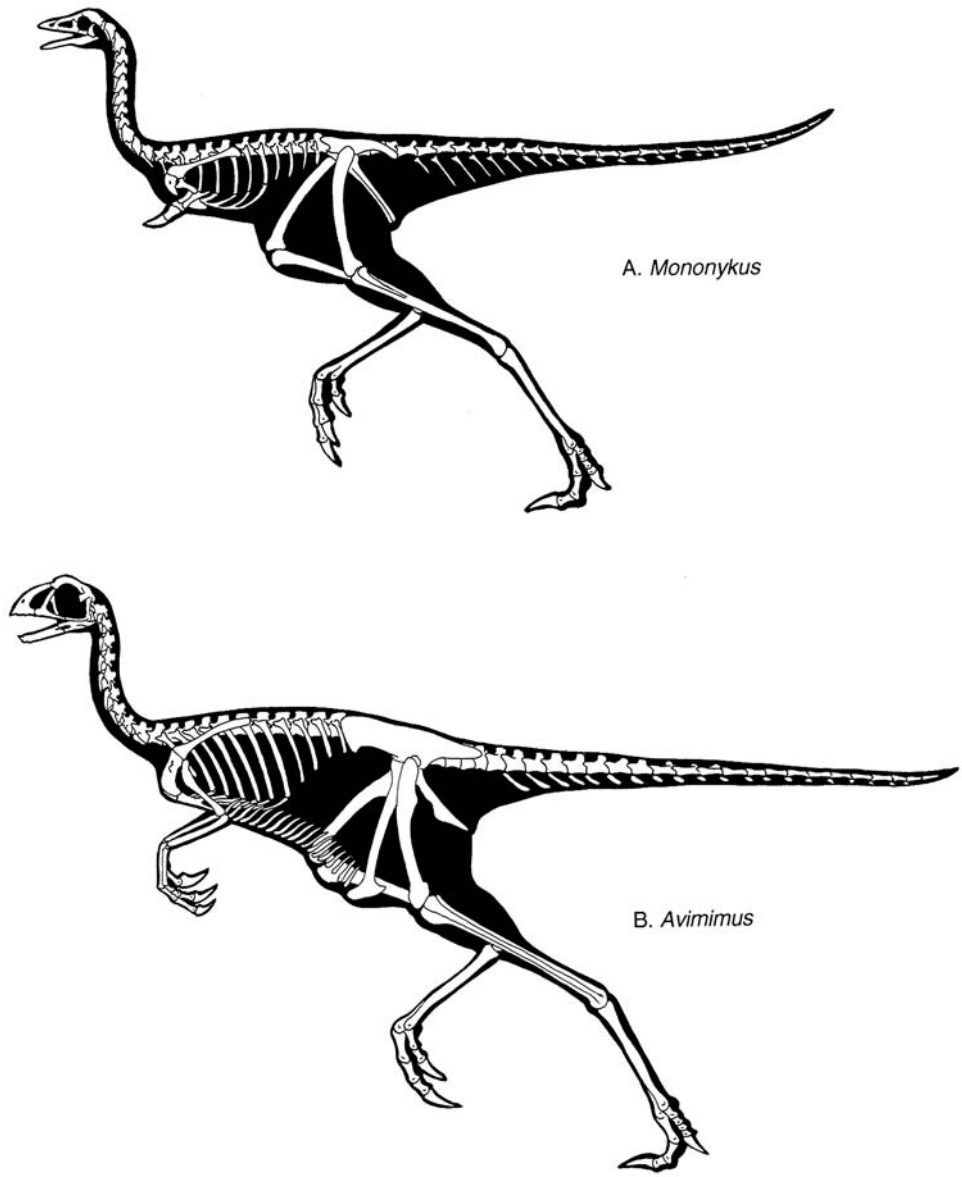


Figure 3.15. Basal maniraptorans from the Late Cretaceous Gobi Desert of Mongolia. A, *Mononykus olecranus*, an alvarezsaurid. B, *Avimimus prorontus*, an oviraptorosaur (after Chatterjee 1997).

Early Cretaceous of China were probably arboreal and developed various stages of contour feathers for primitive gliding (Chatterjee and Templin 2004a, 2012). In several taxa of oviraptorosaurs, prominent cranial crests are common. The absence of teeth and the inferred presence of horny beaks in advanced forms, as well as preservation of gastroliths, or gizzard stones, in *Caudipteryx* suggest that oviraptorosaurs were predominantly herbivores (Paul 2002). They had slender hindlimbs and grasping hands, and rarely exceeded 2 meters in length (Osmolska et al. 2004). The Cretaceous oviraptorosaurs are represented by three clades: the caenagnathids such as *Chirostenotes* and *Caenagnathasia* from North America; avimimids such as *Avimimus* from the Late Cretaceous of Mongolia; and oviraptorids such as *Oviraptor*, *Citipati*, and *Khaan* from the Late Cretaceous Djadokhta Formation at Ukhha Tolgod in Mongolia (Clark et al. 2002).

The Russian paleontologist S. M. Kurzanov described the enigmatic theropod *Avimimus* from the Gobi Desert in 1985 and 1987. He documented in this turkey-sized ani-

mal a suite of avian characteristics that are not present in *Archaeopteryx*. The skull of *Avimimus* is remarkably avian, with the orbit and lower temporal opening confluent (fig. 3.15B). The jugal bar is a slender rod, as is seen in modern birds. The squamosal-quadratojugal bar has been lost in front of the quadrate, making the quadrate free. However, the quadrate is primitive and fused secondarily with the squamosal to lose its streptostyly. The upper temporal arch is intact and retains the postorbital. The palate retains the ectopterygoid bone. The braincase is inflated and modern looking, whereas the occipital condyle is reduced. The skull is about 85 millimeters long, with a large orbit and edentulous jaws, but the premaxilla has toothlike denticles (fig. 3.15).

The cervical vertebrae of *Avimimus* show pleurocoels and hypapophyses. The shoulder girdle is unknown. The humerus has asymmetrical distal ends, and the carpometacarpus is fused like that of modern birds. The pelvis and the hindlimbs, however, are primitively built. The ilium has a prominent antitrochanter and brevis shelf. The two pubes are fused distally, with an expanded foot. The orientation of the pubis is forward and downward, as seen in primitive nonavian theropods. The femur has a spherical head and a well-developed trochanteric crest; the lesser trochanter rises to the level of the greater trochanter. In addition, there is a posterior trochanter, as is seen in some maniraptorans. However, the femoral shaft retains a fourth trochanter, which is a primitive feature. The tibia, fibula, and proximal tarsals are fused distally. The metatarsals are also fused proximally; a splint-like fifth metatarsal is present. *Avimimus* is clearly an unusual theropod, showing a curious mixture of primitive and advanced features. Because of these conflicting characteristics, some paleontologists believe that *Avimimus* may indicate the mixture of two species. Certainly, the skull, cervical vertebrae, and limbs show many avialan attributes. The lack of a shoulder girdle makes it difficult to assess its avian level of organization.

Recent discoveries of several basal groups of feathered oviraptorosaurs such as *Incisivosaurus* (Xu et al. 2002), *Caudipteryx* (Ji et al. 1998), and *Protarchaeopteryx* (Ji et al. 1998) from the Early Cretaceous Jehol Group of China provide critical insights about the lifestyle of these herbivores. *Caudipteryx* had a short, boxy skull with a beaklike snout that retained a few tapered teeth in the upper jaw and was probably an herbivore. The hands and tail supported fans of large contour feathers, each with a central rachis and symmetrical vanes on either side possibly for parachuting from a tree branch to retard a fall (Chatterjee and Templin 2004a, 2012). *Protarchaeopteryx* had long forelimbs with slender hands that supported three fingers equipped with sharp and curved claws, possibly for climbing trees. The hands and tail supported symmetrical contour feathers like those of *Caudipteryx*, possibly for parachuting from a perch. *Oviraptor* from the Late Cretaceous of Mongolia had a highly pneumatized skull ornamented with a crest and toothless jaws. Avian features are so widely distributed in the skeletons of oviraptorosaurs that some researchers (Elzanowski 1999; Maryanska et al. 2002) suggested that these animals might have been the earliest known flightless birds, which branched off after *Archaeopteryx*. However, this conclusion is not supported in more rigorous and phylogenetic studies (Makovicky and Zanno 2011). Oviraptorosaurs had muscular and stubby tails adorned with fan-like feathers at the tips. The bird-like pygostyle has been discovered in *Nomingia* (Barsbold et al. 2000). Most likely the pygostyle evolved independently in oviraptorosaurs and later in pygostylian birds probably for attachment of fan-like tail feathers. The bizarre cranial crests of oviraptorosaurs and terminal tail feathers were possibly used for sexual display to attract a mate. Similarly, bird-like brooding behavior has been documented in another Mongolian oviraptorid, *Citipati*, crouching over its clutch of eggs (Clark et al. 1999).

The oviraptors are considered to be a sister clade to avialans (Xu et al. 2011), but other workers disagree and class them as basal maniraptorans (Turner et al. 2012). Oviraptorosaurs exhibit remarkable similarities with early Chinese avialans such as *Jeholornis* in skeletal structure, skull anatomy (high and boxy), and herbivorous adaptation. The toothless skull of oviraptors is highly modified, with elevated external nares; the premaxilla is deep and larger than the maxilla; the palate extends below the

cheek margin; and the dentary symphysis is fused. The scapula articulates with the coracoid at a 90° angle, which is indicative of flight ancestry. The remiges show contour feathers with symmetrical vanes. Recent work suggests that herbivory may have been common among oviraptorosaurs and early avialans (Zanno and Makovicky 2011).

Paraves

The clade Paraves encompasses all theropods, which are more closely related to early birds (Avialae) than to oviraptorosaurs (Sereno 1999). Recent phylogeny suggests that they include four major subgroups: Scansoriopterygidae, represented by small, arboreal, neoflightless forms such as *Epidexipteryx* and *Epidendrosaurus*; Deinonychosauria, including dromaeosaurids and trodontids; Averaptora, including Tetrapterygidae and Avialae; and Avialae, which includes *Archaeopteryx*, *Jeholronis*, and other pygostylians birds (Turner et al. 2012; Godefroit et al. 2013a, 2013b; Agnolin and Novas 2013). The clade Eumaniraptora as used here includes deinonychosaurs and Averaptora, but excludes scansoriopterygids (fig. 3.16). Paraves shows several synapomorphies such as a retroverted pubis, an extended and flexed coracoid, and a shortened tail. The significant lengthening and thickening of the forelimbs indicates a dramatic shift in forelimb function for rudimentary fight. Most paravians, including all birds, possess asymmetric flight feathers to generate lift, but several groups became secondarily flightless and fully arboreal (Chatterjee and Templin 2012).

Scansoriopterygidae (meaning "climbing wings") is a family of arboreal paravians known from the Middle-Late Jurassic Daohugou beds of Inner Mongolia, northern China, with their extremely elongated third fingers and downy feathers. They possessed several bird-like attributes in the skeleton. The exact placement of this clade is uncertain and controversial. Several phylogenetic studies have put scansoriopterygids as basal members of avialans (Zhang et al. 2008; Xu et al. 2011), or as basal members of paravians (Turner et al. 2012; Godefroit et al. 2013a, 2013b). Because of their robust and hyperelongated third finger and secondary loss of flight, scansoriopterygids represent a bizarre lineage of paravians with reduced plumages.

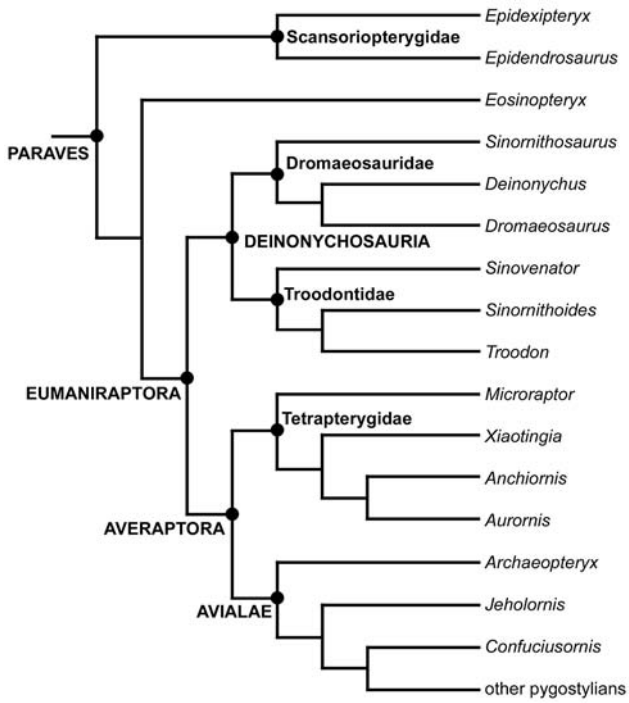


Figure 3.16. Cladogram showing suggested interrelationships of major clades of paravians (simplified from Turner et al. 2012; Godefroit et al. 2013a, 2013b; Agnolin and Novas 2013).

With the secondary loss of flight, it is difficult to ascertain whether certain characters are considered truly plesiomorphic, or as derived reversals that only resemble primitive conditions secondarily (Czerkas and Yuan 2002). In my estimation, they are basal arboreal paravians, which are not closely related to birds. So far, they are the only noneumaniraptoran paravians known (Turner et al. 2012; Godefroit et al. 2013b).

Scansoriopterygids provide significant information on the temporal framework of paravian divergence and offer clues on bird evolution. They are among the smallest feathered coelurosaurs known; the juvenile specimens of *Epidendrosaurus* (= *Scansauriopteryx*) are about the size of a sparrow (Czerkas and Yuan 2002; Zhang et al. 2002), while the specimen of *Epidexipteryx* would be about the size of a pigeon (Zhang et al. 2008). The skull is high in lateral view, the external naris is positioned high on the snout, and the parietal is proportionately long. They are characterized by their climbing adaptations as evidenced by their long hands with extremely elongated third fin-

gers (outer digits) and strongly curved foot claws, as well as reduced plumages. Most likely they lacked flight feathers, but retained downy feathers throughout their bodies and became secondarily flightless (see chapter 14). As Paul (2002) has suggested, the loss of flight is a recurrent theme in the evolution of birds. Since *Epidendrosaurus* represents a juvenile specimen, many characters were not fully expressed. As a result we use *Epidexipteryx* as a representative of this enigmatic neoflightless clade of scansoriopterygids.

Epidexipteryx hui is known from the Middle-Late Jurassic Daohugou beds of Inner Mongolia, sporting bizarre, elongate, ribbon-like tail feathers (Zhang et al. 2008). *Epidexipteryx* was a small, primitive paravian, about the size of a pigeon, about 25 centimeters long including its elongated tail feathers. The skull is lightly built and high as in oviraptorosaurs with a retracted external naris, a large antorbital opening, a large circular orbit, a T-shaped lacrimal with a large pneumatic fossa, a large mandibular fenestra, a slender jugal bar, and diapsid arches; the squamosal-quadratojugal bar in front of the quadrate is breached, allowing some backward movement of the quadrate. The frontoparietal region is dome-shaped, indicating an expanded braincase. The sharp, conical teeth are present in the front of the jaws; the unusually long front teeth are highly procumbent (fig. 3.17).

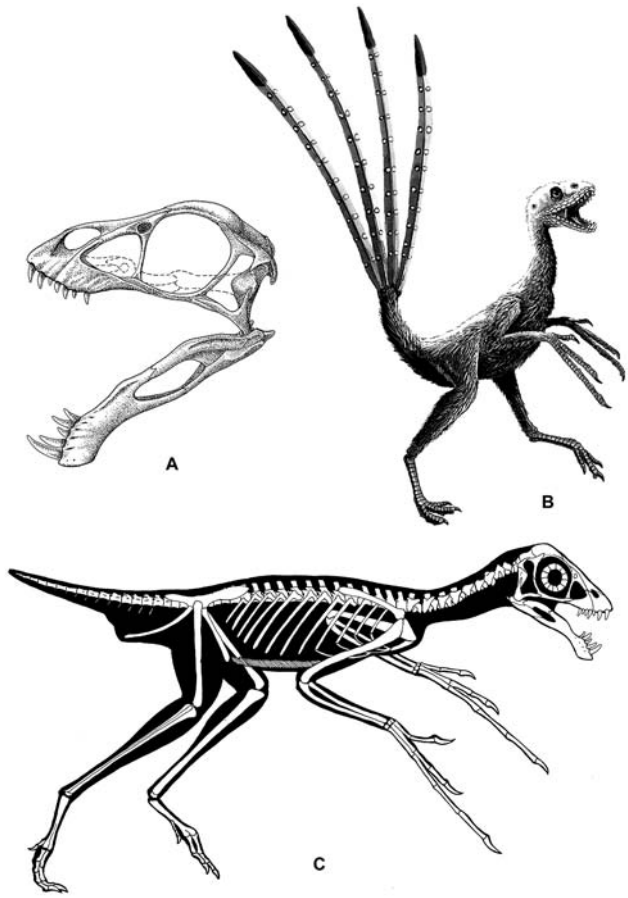


Figure 3.17. *Epidexipteryx hui*, a scansoripterygid from the Daohugou beds of Mongolia. A, skull restoration; B, life restoration; C, skeletal restoration (Zhang et al. 2002).

There are probably 9 cervicals, 14 thoracic vertebrae, 7 sacrals, and more than 16 caudals. The scapula is short, and the coracoid is subrectangular. The sternum is small and convex anteriorly, and lacks fusion at the midline. The forelimbs are elongated; the humerus is as long as the femur, the ulna is bowed posteriorly, and the manus is long with a highly elongated third finger and is equipped with highly recurved claws for scansorial adaptation. The pelvis is propubic; the ilium has a long preacetabular process and a small pubic peduncle; the ischium is expanded and longer than the pubis, an unusual disparity configuration among maniraptorans.

Epidexipteryx lacked flight feathers and became secondarily flightless. The body was covered with simple downy feathers to keep it warm. The living kakapo parrot of New Zealand, a flightless species, is a modern analogue of *Epidexipteryx*. The kakapo has a downy plumage covering like *Epidexipteryx*; it can climb trees and parachute down using its wings for balance and braking. The most striking feature in *Epidexipteryx* is the presence of four super-long strap-like tail feathers, tightly attached to the last ten caudal segments from a membranous base. The posterior caudal series was stiff like the elongated, incipient pygostyle in some basal birds, but not fused to each other. The tail appears to be flexible at its base but rigid at its tip where feathers are attached. The most likely use for a fan-like, feather-tipped tail is for courtship display. *Epidexipteryx* would shake its tail feathers to charm its potential mate or threaten an enemy. In modern birds ornamental tail feathers as seen in peacocks or birds of paradise are for sexual display. Most likely

Epidexipteryx used these elongate tail feathers to charm a mate, thus highlighting the evolutionary power of sexual selection. Each feather has a central rachis and unbranched vanes, which are not branched into individual filaments, but consist of a single ribbon-like sheet. From the showy tail of *Epidexipteryx* it has been suggested that feathers initially might have evolved for sexual display and were then later co-opted for flight (Chatterjee and Templin 2012).

Did this attractive tail have any aerodynamic function? These stiff tail feathers along with wings could be used for parachuting from the tree branches or retarding falls. *Epidexipteryx* evolved from flying ancestors but became secondarily flightless. Its contemporary, the nonavian theropod *Anchiornis*, did possess flight feathers (see chapter 14). Many of the features suggest that *Epidexipteryx* was an arboreal bird that lived in the trees for hunting insects and avoided hungry predators on the ground. The inflated braincase of *Epidexipteryx* suggests that it lived in a three-dimensional world among trees like the modern kakapo parrot.

Eumaniraptora

Eumaniraptorans include two clades, Deinonychosauria and the newly defined Averaptora (Agnolin and Novas 2013). The actual shared derived characters that unite them as a whole are somewhat problematic because of the uncertainty of the position of *Archaeopteryx* (Xu et al. 2011). Usually, eumaniraptorans have small body size, long arms, very large hands, a backward-facing pubis, long leg feathers, and a tail that is mobile near the base but is stiff the rest of its length.

Deinonychosaurs ("fearsome claws") are known from the Late Jurassic and Cretaceous periods (fig. 3.14). They were the true raptors among theropods with a retractable pedal digit 2. Because of their close anatomical similarities and possession of asymmetric flight feathers, deinonychosaurs are generally regarded as the close sister group of *Archaeopteryx* and other avialans (Ostrom 1969). They share the following synapomorphies: elongated wings, sickle-shaped second toe claws, and a triangular lateral exposure of the splenial along the edge of the lower jaw. The deinonychosaurs have gracile skulls, a carnivorous diet, and asymmetric flight feathers; all these features possibly evolved secondarily in deinonychosaurs. The deinonychosaurs include two clades: Dromaeosauridae and Troodontidae. Large deinonychosaurs such as *Deinonychus* and *Velociraptor* became secondarily flightless from their flying ancestors (Paul 2002), attained large size, reverted to fully terrestrial habits, and assumed the role of stealth predators.

The dromaeosaurids are small to medium-sized Late Jurassic to Cretaceous maniraptorans from China, Mongolia, North America, and South America and include several genera such as *Sinornithosaurus*, *Bambiraptor*, *Velociraptor*, *Unenlagia*, *Rahonavis*, and *Troodon*. Ostrom (1976a, b) recognized the close relationship between dromaeosaurs such as *Deinonychus* and early birds such as *Archaeopteryx*, which became the foundation of the theropod hypothesis of bird origin. The skeletons of dromaeosaurs and *Archaeopteryx* are almost undistinguishable because of flight-related adaptations. Many of the small dromaeosaurs from China had developed flight feathers and are comparable in body size and features to *Archaeopteryx*.

The troodontids were small to medium-sized theropods, which are known from North America, China, and Mongolia. They had highly pneumatized skulls, unusually large orbits, and expanded brains among theropods, comparable to those of living flightless birds (fig. 3.12). They had coarsely serrated teeth, large denticle size, and U-shaped jaws that suggest that some species might have been omnivores. Some unusual fossils such as *Mei* and *Sauronithoides* were associated with nests and embryos that indicate that these animals roosted like birds, with their heads tucked under their forelimbs. A duck-sized troodontid is *Mei* from the Jehol Group, which was found in the ash bed in a bird-like sleeping pose (fig. 12.7C).

Averaptora

The rapid discovery of so many bird-like paravians from China such as *Xiaotingia*, *Anchiornis*, *Aurornis*, *Eosinopteryx*, *Epidexipteryx*, and *Epidendrosaurus* has spurred debate over how to distinguish between the creatures that truly were early birds and those that merely look like

good candidates for archaic avialans. These animals are anatomically very similar and lie so close to the avialan ancestry that it is difficult to tell exactly where they fit because our definition of early birds is largely arbitrary, guided by the characters of *Archaeopteryx*.

Agnolin and Novas (2013) erected a new clade, Averaptora, to include four-winged maniraptorans such as *Microraptor*, *Anchiornis*, and *Xiaotingia* as well as *Archaeopteryx* and other avialans. Here I propose a new family, Tetrapterygidae, to include these four-winged paravians—*Microraptor*, *Xiaotingia*, *Anchiornis*, and *Aurornis* (fig. 3.16). Thus Averaptora broadly includes two clades: Tetrapterygidae and Avialae. Instead of two wings, the tetrapterygids must have used four wings to stay aloft with a biplane wing configuration (Chatterjee and Templin 2007a).

Several four-winged maniraptorans from the Late Jurassic Tiaojishan Formation of China such as *Xiaotingia* and *Anchiornis* share several features with *Archaeopteryx* and have profound implications for the origin of birds and the evolutionary appearance of avialan features; as such, their phylogenetic positions within paravians are fluid and the compositions of avialans are highly contested in recent times (Xu et al. 2011; Godefroit et al. 2013a, 2013b; Turner et al. 2012; Agnolin and Novas 2013) (see chapter 4). It is hoped that continued phylogenetic studies of paravians will resolve some of the relationships of these controversial taxa.

Traditionally, *Microraptor gui* from the Early Cretaceous of China is grouped as a member of the dromaeosaurs, but Agnolin and Novas (2013) considered this biplane maniraptoran a member of the averaptorans. Several specimens of *Microraptor* are exquisitely preserved, exhibiting long contour feathers not only on their wings but also on their lower legs and feet. This four-winged averaptoran had developed long, asymmetric feathers on its hands and feet that suggest that it had a biplane wing design and could glide efficiently (fig. 12.7B). Pigment-containing cells called melanosomes from a *Microraptor* fossil show that the animal had a predominantly glossy iridescent sheen in hues of black and blue, like a crow, probably for sexual display (Li et al. 2012).

Unlike *Microraptor*, *Xiaotingia*, *Anchiornis*, and *Aurornis* are known from the Late Jurassic Tiaojishan Formation of western Liaoning, China (fig. 4.5). The initial analysis of Xu et al. (2011) suggests that *Xiaotingia* and *Anchiornis* formed a clade with *Archaeopteryx* called Archaeopterygidae within deinonychosaurs. However, later workers have challenged this analysis (Godefroit et al. 2013a, 2013b; Turner et al. 2012; Agnolin and Novas 2013). Both *Xiaotingia* and *Anchiornis* had a biplane wing design like that of *Microraptor*, whereas *Archaeopteryx* had a monoplane design (see chapter 12). In contrast, *Aurornis* probably became secondarily flightless with reduced wings.

Aurornis is beautifully preserved and has much the same anatomical features as *Xiaotingia*, *Anchiornis*, and *Eosinopteryx*. They all lived at the same time in the same place in northeastern China. However, the authenticity of the solitary specimen of *Aurornis* is controversial because the fossil came from a dealer, and its provenance is uncertain (see chapter 4). Many paleontologists believe that *Aurornis* might be another variant of *Anchiornis*. In this study, *Xiaotingia*, *Anchiornis*, and *Aurornis* are regarded as small, feathered tetrapterygids, while *Archaeopteryx* is placed as a basal member of Avialae in the traditional sense (fig. 3.10).

Avialae

The phylogenetic position of *Archaeopteryx* within Paraves has become highly controversial in recent decades. For 150 years *Archaeopteryx* has been iconic as the most basal bird within Avialae, but the discovery of the closely related *Xiaotingia* from the Middle-Late Jurassic of China led Xu et al. (2011) to conclude that *Archaeopteryx* is no longer a bird according to new phylogenetic assessment (see chapter 4). *Xiaotingia* moved *Archaeopteryx* from the avialan category and placed the duo with the deinonychosaurs in a separate family, Archaeopterygidae, along with *Anchiornis*. A quick response using a different method of phylogenetic analysis reaffirmed the avialan status of *Archaeopteryx* (Lee et al. 2012). Another recent phylogenetic analysis supports the conclusion that *Archaeopteryx* is a deinonychosaurian theropod instead of a primitive avialan with the incorporation of *Eosinopteryx*, another

new, feathered paravian from the Late Jurassic of China (Godefroit et al. 2103a). With the discovery of another new paravian, *Aurornis*, from the Middle-Late Jurassic of China, Godefroit et al. (2013b) contradicted their earlier conclusions and put *Archaeopteryx* back on its traditional roost as an avialan. In this new analysis, *Aurornis*, *Anchiornis*, *Archaeopteryx*, and *Xiaotingia* are all identified as basal members of Avialae. In contrast, Turner et al. (2012) placed *Anchiornis* and *Xiaotingia* within the troodontids.

In my discussion, I have included *Archaeopteryx*, *Jeholornis*, and other pygostylians within avialans. Many of the synapomorphies of avialans, such as forelimb elongation, hindlimb reduction, tail reduction, and modifications of the pelvis associated with a crouched posture, are associated with flight-related morphology. There are several modifications in the skull providing increased pneumaticity as well as more extensive ossification. Some of the skull characters include the following: (1) a dorsoventrally high premaxilla that is significantly larger than the maxilla; (2) a dorsally positioned external naris; (3) a dorsoventrally tall antorbital fossa; (4) a jugal with a relatively vertical postorbital process and a long quadratojugal process; (5) a relatively long parietal; (6) an anteriorly downturned and dorsally convex mandible; (7) a large external mandibular fenestra; (8) enlarged anterior teeth; (9) a posterior tympanic recess that extends to the opisthotic; and (10) separate parietals.

Evolutionary Trends in Avialans

The genealogy of Theropoda (fig. 3.10) presents several evolutionary trends in the acquisition of avialan characters and their physiological and functional correlates:

1. *Miniaturization*. A decrease in body size (ranging from 500 grams to 1 kilogram) is a trend in arboreal coelurosaurs that culminates in avialans.

2. *Arboreality*. Small size and clawed wings conferred an arboreal lifestyle on many coelurosaurs. However, some groups reverted secondarily to a terrestrial lifestyle (neoflightless condition) and became large.

3. *Development of feathers*. Although feathers might have developed at the base of the dinosaur radiation, various stages of feathers developed in coelurosaurs, including downy and contour feathers. Some contour feathers became the large and asymmetric flight feathers of the wings, feet, and tail. Many of the feathers had bright colors, implying that they might have evolved initially for species recognition and sexual display and were later coopted for flight.

4. *Modification of the skull*

a. Tooth reduction and change in feeding style. Although theropods are dominantly carnivores with formidable teeth, there is a reverse trend in the gradual loss of teeth with the formation of a beak and change in feeding strategy from carnivory to herbivory in oviraptorosaurs and some early avialans such as *Jeholornis* (fig. 3.15).

b. Brain enlargement. There is a progressive enlargement in relative brain size as reflected in the increase in the encephalization quotient from 0.16 to 0.54. Both cerebral hemispheres and cerebellum were enlarged, touching each other dorsally, thus displacing the optic lobes laterally and somewhat ventrally (fig. 3.12).

c. Modification of the otic capsule. The otic capsule of the braincase of *Coelophysis* is primitively built in archosaur fashion; the metotic foramen occurs just behind the fenestra ovalis for the exit of cranial nerves IX–XI and the posterior branch of the jugular vein. In tetanuran and coelurosaurian lineage, the otic capsule is modified with the backward diversion of the metotic canal with the ossification of the metotic flange, the opening of the vagus nerve canal in the occiput, and the development of the pseudorotunda in place of the metotic foramen (fig. 3.13).

d. Development of three tympanic pneumaticities—rostral, dorsal, and caudal—in the ear region. In basal theropods, such as *Syntarsus*, both rostral and caudal tympanic recesses are present, and these two recesses have been identified in coelurosaurs and maniraptorans; however, the dorsal tympanic recess is derived, and is so far known in *Archaeopteryx*, *Protoavis*, and avialans (Chatterjee 1991).

e. Flexibility of the quadrate-quadratojugal articulation to achieve prostyly, as seen in some juvenile maniraptorans and avialans.

f. Intramandibular joint and lateral spreading, a trait present in all theropods and birds that helps to increase

the diameter of the throat during the swallowing of large food items.

5. *Vertebral column*

a. Pneumatization. The air-filled spaces in the theropod skeleton, as is evident from the development of pleurocoels (pneumatic holes on the side of the cervical and anterior dorsal vertebrae), made the body light and allowed room for soft tissue air sacs that served as bellows to ventilate the lungs.

b. Synsacrum. The primitive theropods such as *Coelophysis* had five sacral vertebrae. There is a progressive increase in the number of sacral vertebrae from five to seven or eight in early avialans.

c. Tail. Two features evolved in the modification of the bony tail from basal theropods: stiffening of the tail in tetanurans and reduction of tail vertebrae from forty-four (in *Coelophysis*) to twenty-two (in *Archaeopteryx*). The long bony tail of *Archaeopteryx* and *Jeholornis* supported frond-like feathers, which are better suited for stability than a lifting surface (fig. 3.18). The reduction in the number of tail vertebrae might be associated with a reduction in caudofemoral musculature for femoral retraction, which was abandoned in avialans as the femur became horizontal; the main hindlimb movement was transferred from the hip joint to the knee joint in avialans (Gatesy 1990).

The shortening of the tail and the rod-shaped pygostyle first appeared in Pygostylia such as *Confuciusornis* that supported a tuft of feathers that could enhance aerial turning. The loss of a long bony tail conferred instability but maneuverability in pygostylians. In ornithurine and modern birds, the pygostyle becomes plowshare in shape to support fan-like feathers for maneuvering flight that can alter lift and manipulate the flight surface (Gatesy and Dial 1996). Here the tail and wings work together during acrobatic flight.

d. Uncinate process. The ribcage is strengthened with the development of short bony struts, called uncinate processes, which interconnect one rib with the next and thus stabilize the shoulder musculature.

6. *Shoulder girdle*

a. Strap-like scapula.

b. Strut-like coracoid; elongation of the coracoid with the development of the biceps tubercle, precursors to the avian procoracoid (fig. 3.19).

c. Change of scapulocoracoid articulation from an obtuse to an acute angle.

d. Ossification of the sternum and the development of a keel for anchoring flight muscles.

d. Triosseal canal at the trijunction of the scapula, coracoid, and furcula for the supracoracoideus pulley to elevate the wing during upstroke.

e. Development of a U-shaped furcula.

7. *Wings*

a. Elongation of the forelimbs; the forelimbs became longer than the hindlimbs to form a large flight surface.

b. Highly recurved claws for climbing.

c. Fused semilunate distal carpal bones allowing swivel wrist joints during climbing and flying (fig. 3.20).

d. Reduction in the number of fingers to three digits.

8. *Pelvic girdle*

a. Elongation of the iliac blade both anteriorly and posteriorly to accommodate a large number of sacral vertebrae (fig. 3.21).

b. Retroverted pubis; backward rotation of the pubis and ischium.

c. Fusion of the ilium, ischium, and pubis with the sacral vertebrae to form the synsacrum.

9. *Hindlimbs*

a. Tibia longer than the femur.

b. Loss of the femoral fourth trochanter.

c. Fibula slimmer and shorter than the tibia.

d. Mesotarsal ankle joint (fig. 3.22).

d. Fused astragalocalcaneum.

e. Progressive enlargement of the ascending process on the astragalus.

f. Functional tridactyl foot; loss of the fifth digit.

g. Anisodactyl foot.

To Fly or Not to Fly: Neoflightless Coelurosaurs

Flightless birds such as ostriches, emus, cassowaries, rheas, kiwis, and penguins lack the ability to fly, relying

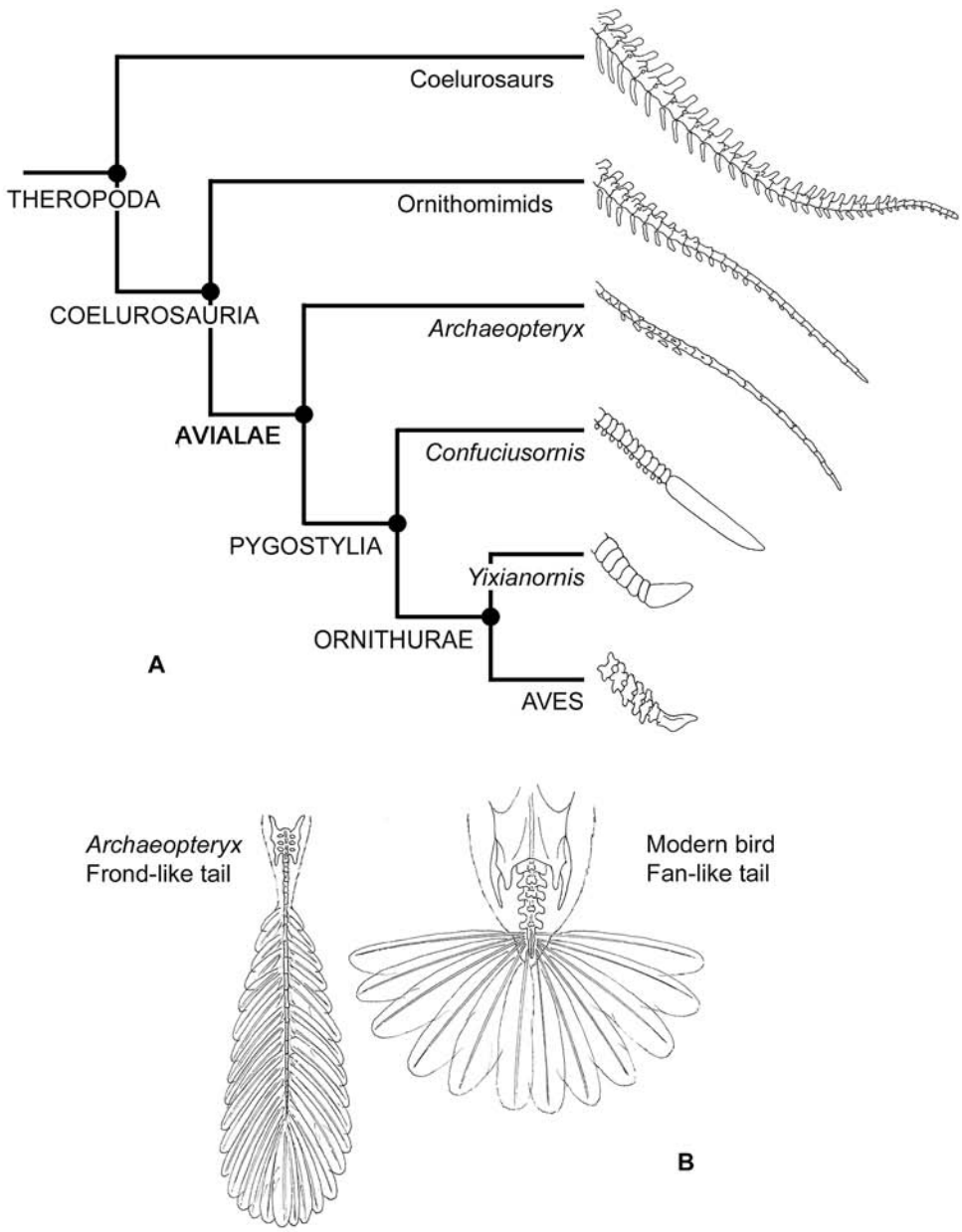


Figure 3.18. Trend in tail shortening in theropods during evolution of flight. A, cladogram showing the truncation of the tail in the theropod lineage with reduction in caudal vertebrae number from forty-four (in ceratosaurs) to twenty-two (in *Archaeopteryx*). In *Archaeopteryx*, the relatively short and narrow bony tail supports frond-like tail feathers, which are better suited to stabilization than lift production. In basal pygostylians, such as *Confuciusornis*, the number of vertebrae in the bony tail is considerably reduced and the final six are fused to form a pygostyle, which is rod-shaped and supports a short tuft of thin feathers. The short tail makes pygostylians less stable but more maneuverable for steering during flight. During terrestrial locomotion, the hindlimbs and tail were functionally decoupled. In Ornithurae such as *Yixianornis* and modern birds, the pygostyle becomes plowshare in shape and supports fan-like tail feathers that can alter lift and manipulate the flight surface; wings and tail work in concert during flight. B, tail design in *Archaeopteryx* and modern birds; the frond-like arrangement of the tail feathers of *Archaeopteryx* produced only a fraction of the lift generated by the fan-like tail design of modern birds (modified from Gatesy and Dial 1996).

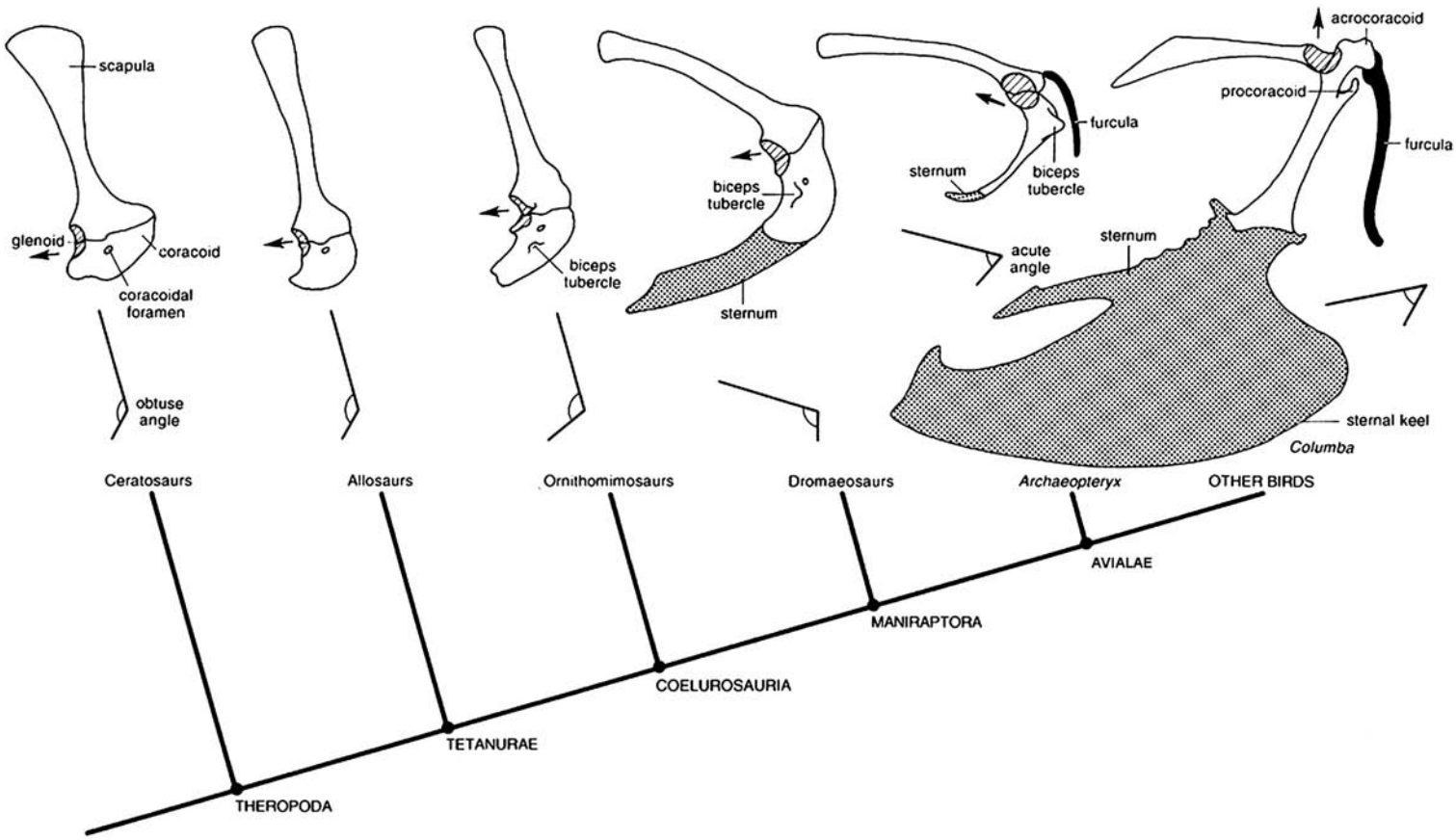


Figure 3.19. Right lateral diagrammatic view of the shoulder girdle of theropods showing the evolution of the avian condition. The cladogram exhibits a progressive change in the angle of articulation between the scapula and the coracoid from ceratosaurs (*Syntarsus*), through allosaurs (*Allosaurus*), ornithomimosaurs (*Struthiomimus*), dromaeosaurs (*Deinonychus*), and *Archaeopteryx*, to modern birds (*Columba*). An obtuse angle of scapulocoracoid articulation is found in nonflying outgroups, but the acute angle is characteristic of flying birds. In this progression, the coracoid becomes more and more deep and the biceps tubercle migrates rostrally and dorsally to form the avian acrocoracoid process (Ostrom 1976b). The sternum is known in dromaeosaurs and might have evolved for climbing. Although the sternum was unossified in most specimens of *Archaeopteryx*, there might be a small sternum in *Archaeopteryx bavarica* (Wellnhofer 1993); the apparent cartilaginous sternum in *Archaeopteryx* lacks the strength of those in modern birds that anchor powerful flight muscles. A large sternal keel is characteristic of flying birds, with a furcula between the two shoulder girdles. The keel provides an area for the attachment of flight muscles. The distribution of the furcula among nonavian theropods is uncertain. It is certainly present in ceratosaurs such as *Segisaurus* (Camp 1936), oviraptorosaurs (Barsbold 1983), and several maniraptorans.

instead on their ability to run or swim. Many characters in their anatomy indicate very clearly that flightless birds evolved from flying ancestors. They still retain a large brain, a weight-saving toothless beak, fused wing bones, a horizontal femur, use of the knee joint rather than the hip joint for propulsion, heterocoelous cervical vertebrae and a pygostyle, and the distribution pattern of degenerate feathers in the wings identical to that of true flight feathers. The evolution of a flightless condition is a common theme in the history of birds. Many of these birds became flightless and began to explore the ground when it became safe to do so. They became efficient runners with their long legs to elude predators or increased their size.

Flight is an expensive endeavor in terms of energy and birds do not travel by air if it is safe for them to do so by land. Because of birds' independent and dual mode of locomotion, flying by wings and walking by legs, flight-

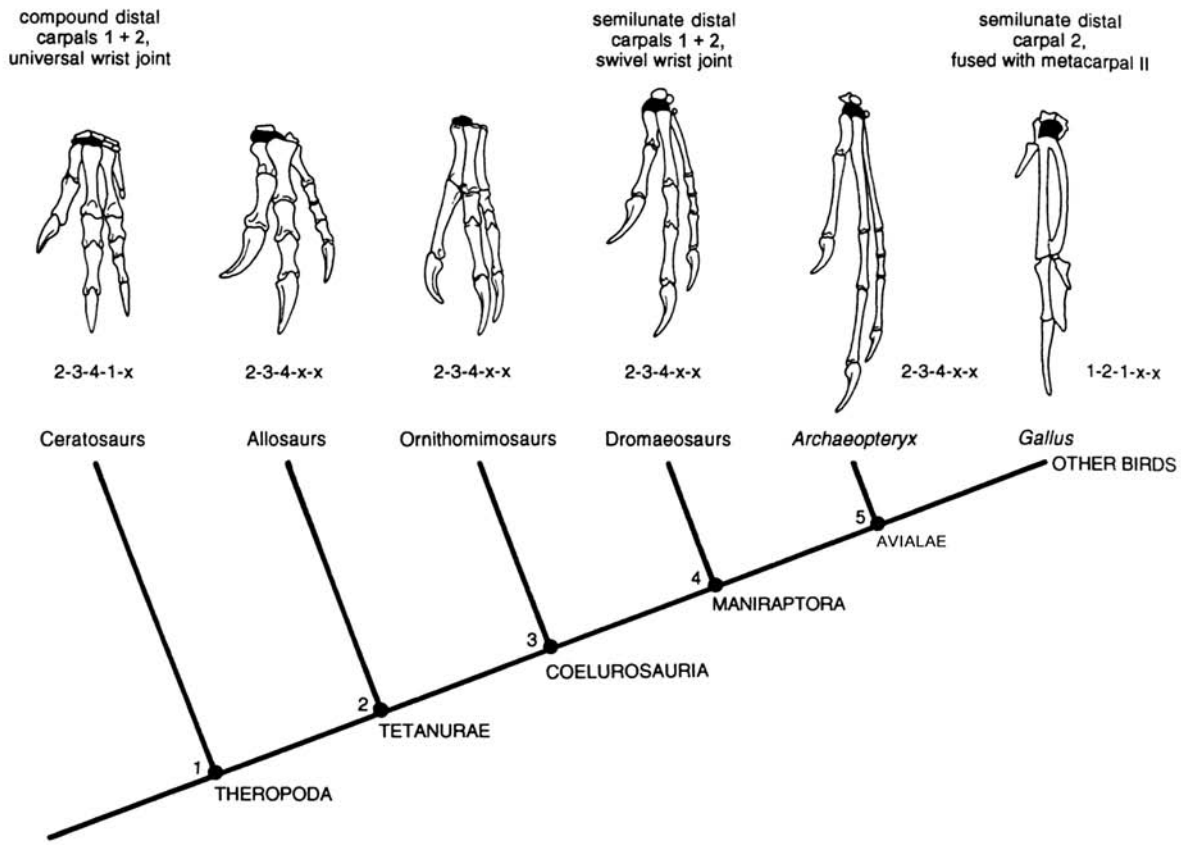


Figure 3.20. Diagrams of the left carpus and manus of theropods showing the evolution of the avian hand. The modification of distal carpals 1 and 2 (shown in black) is the key to the structure of the avian wing. In nonmaniraptoran theropods (such as ceratosaurs, allosaurs, and ornithomimosaurs), the carpal bones are small and numerous, permitting a wide range of motion (universal joint). In these groups, distal carpals 1 and 2 are fused into a compound bone that articulates distally with the first two metacarpals. In maniraptorans such as dromaeosaurs and *Archaeopteryx*, this compound bone develops a curved, rolling articular surface (the semilunate carpal of Ostrom 1979) for the proximal carpals, thus permitting restricted movement of the hand in the plane of the forearm. This swivel wrist joint evolved initially for climbing trees and later was co-opted for flight. It allows folding of the manus along the side of the body when not in use during terrestrial locomotion. In later birds, the semilunate carpal consists of a single bone, distal carpal 2, which becomes fused with metacarpal II to form part of the carpometacarpus. The cladogram also indicates a progressive reduction in the number of digits and phalanges toward the avian condition. The phalangeal formula code is after Padian (1992); 0 indicates metapodials supporting no phalanges and x indicates digits that are completely lost.

lessness does not hinder their movement on land or in water. For instance, any trend toward increasing mass must stop at 70 kilograms, as in *Argentavis*, the largest flying bird from the Miocene of Argentina (Chatterjee et al. 2007), or else continue with the loss of flight, as in the ratites. Flightlessness is a recurrent theme in avian evolution, probably to save energy. True flightlessness, in which all capacity for flight is lost and usually the wings are reduced, is pervasive in birds from a wide range of different taxa. Flightlessness is common in island birds where there are no natural predators. However, flightlessness in continental birds is generally compensated by size increase, as exemplified by ratites. Large size allows stature, longer strides, cursorial ability, better foraging strategy, and natural protection from predation.

All birds are flightless when they are small chicks, and the hatchlings of flying birds show features similar to those that characterize adult flightless birds. Paedomorphosis, the retention of juvenile characters during development, has been a major component of the evo-

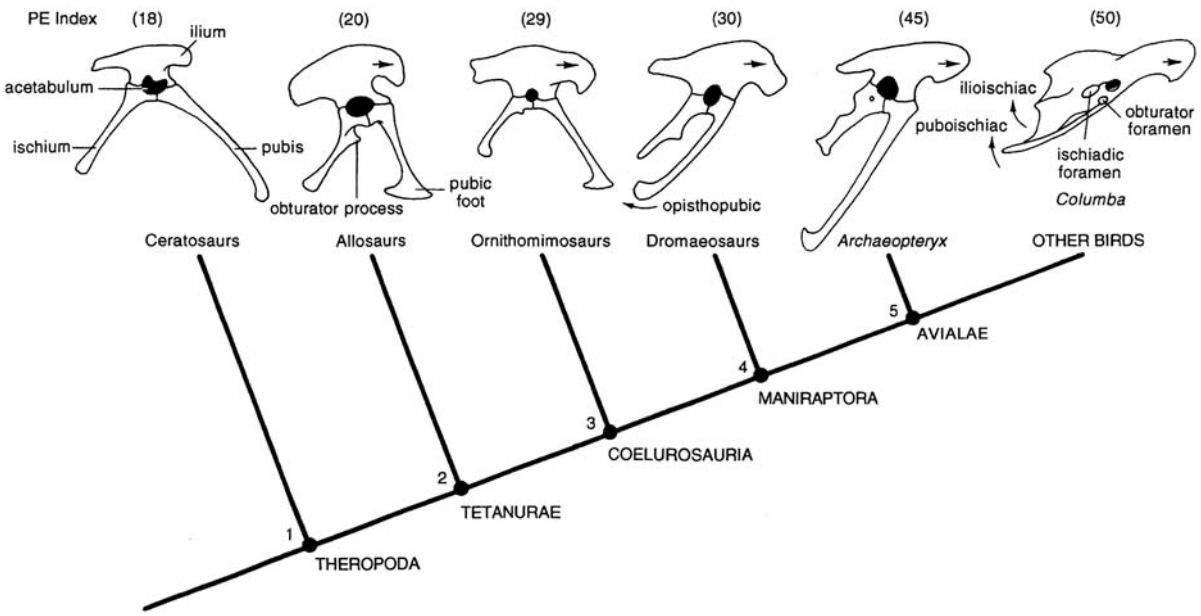


Figure 3.21. Right lateral views of the pelvic girdles of theropods showing the evolution of the avian hip. The cladogram shows the progressive enlargement of the preacetabular process, which is quantified in the preacetabular elongation (PE) index (preacetabular length of ilium rostral to pubic peduncle X 100/total length of ilium). The cladogram also depicts the development of the pubic foot in the tetanuran (allosaurs) stage and gradual rotation of the pubis in a backward direction (the opisthopubic condition) in the maniraptoran (dromaeosaurs) stage. The backward rotation of the pubis may be linked to adaptation for climbing. In more derived birds (Aves), the ischium is also rotated backward to fuse with the ilium and enclose the ilioischiadic foramen.

lution of flightless birds, especially in the reduction of the flight apparatus. These features include a flat sternum without a ventral keel; small wings; disproportionately short distal wing elements; an obtuse angle of articulation between the scapula and the coracoid; a broad, unossified region between the ilium and the ischium; and downy, juvenile-like feathers. Although evolution of flight took millions of years to perfect, flightlessness could be achieved much more rapidly by controlling the switches of development in *Hox* genes.

Greg Paul (2002) has suggested that coelurosaurs repeatedly abandoned flight during their early evolution of flight. This seems quite possible because of two clusters of body size. During the origin of flight, miniaturization of the avian ancestors was the major stimulus to lighten their bodies, thus requiring less energy to propel them against the forces of gravity, both in trees and in the air. Side by side terrestrial forms show large body size. If we start from the feathered coelurosaurs in the theropod cladogram, we see this two distinct size dichotomy—small versus large—in each clade. Smaller species (≤ 1 kilogram) were possibly arboreal, pursuing and improving flight, whereas larger species (10–30 kilograms) were fully terrestrial. There were several events of gigantism associated with flightlessness in the coelurosaur lineage (Turner et al. 2007). Scansoriopterygids became obligatorily arboreal. Similarly, several deinonychosaurs with the development of large metatarsal feathers such as *Microraptor* and *Anchiornis* preferred an arboreal lifestyle because large foot feathers would hinder terrestrial locomotion.

Parapatric Speciation and the Origin of Birds

What was the trigger that led terrestrial theropods to become aerial birds? I suspect parapatric speciation and vertical niche partitioning may be the prime drivers for the evolution of birds from theropod ancestors. Ernst Mayr of Harvard University developed the concept of parapatric speciation. Parapatric speciation occurs along an environment gradient where two parapatric (adjacent) popu-

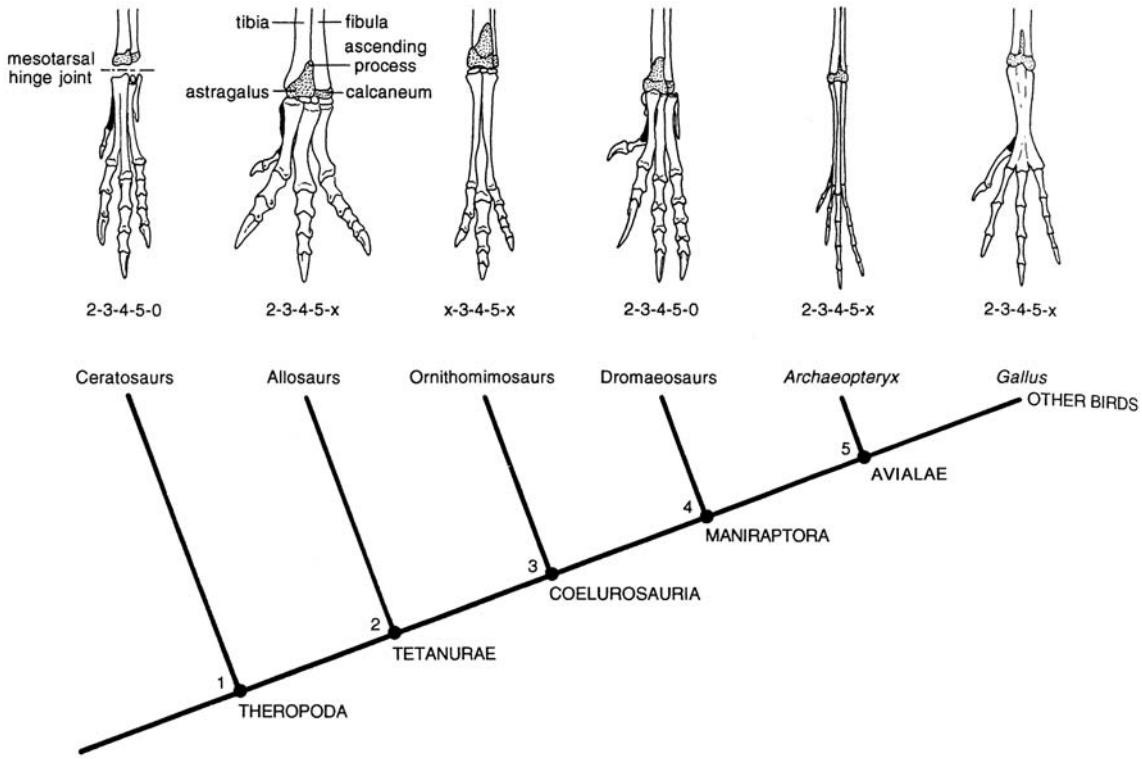


Figure 3.22. Diagrams of the left tarsus and pes depicting the evolution of the avian foot. In theropods, the ankle joint is mesotarsal; the astragalus develops a characteristic ascending process in front of the tibia, a feature first observed by Huxley (1868a). The ascending process provides extra support for locking the tibia with the astragalus. The progressive enlargement of the ascending process in the theropod lineage may be linked to improvement in the cursorial adaptation. In hesperornithiforms and neognathous birds, the ascending process ossifies as a separate element (the pretibial bone) in young individuals but becomes fused with the calcaneum in adults; in nonavian theropods and palaeognaths, on the other hand, the ascending process is not separate but is always fused with the astragalus. There is a progressive distal shift of metatarsal I from basal theropods to birds. In birds, metatarsal I (in black) is attached farther distal to metatarsal II, and the first digit becomes anisodactyl. The primitive phalangeal formula is retained in the first four digits in birds, but the fifth digit is lost.

lations are subject to strongly divergent selection regimes because of separate niches. Numerous distributions of closely related species are known in which species are separated by parapatric borders. The reduced gene flow will often produce a cline in which variation of evolutionary pressure causes a change to occur in allele frequencies within the gene pool between two populations. In parapatric speciation, there is only partial separation of the zones of two diverging populations that are pulled apart by natural selection through different ecological factors. A large population may be spread across a wide range of local environments that slightly differ from each other. On the edge of such a range, small local groups may be strongly affected by natural selection, tending to adapt them to their different niches. Some finches of the Galapagos Islands provide a classic example of parapatric speciation because of altitudinal gradients—the evolutionary process through which a single lineage gives rise to two species occupying different ecological niches (Grant and Grant 2008). There is a slight tendency for ground finches at high altitudes to be larger than those at low altitudes. Similarly, the most favorable circumstances for parapatric speciation in theropods are niche partitioning between ground theropods and tree theropods that might have led to genetic divergence, phenotypic and behavioral changes, and speciation.

The Daohugou and Jehol biota clearly suggest that avialans and their theropod antecedents coexisted in the

forest environment around lakes, but possibly occupied different niches, as indicated by their size, anatomy, and adaptation. The stimulus for bird evolution might be linked to the arboreal lifestyle of a small population of coelurosaurs, which became peripherally isolated from the large population of terrestrial forms. This is an example of parapatric speciation when a small population of long-armed theropods with swivel wrist joints began to climb trees and invaded new arboreal niches probably to avoid predators at the periphery of the original geographic range. These little coelurosaurs became the masters of life in the trees, primarily due to their small size and grasping hands and feet. Life in trees demanded a constant stream of body adjustments that led to balance and coordination. Over time the little colony of arboreal forms inbred, local conditions exerted their selective pressures, and descendants became increasingly different from their ancestral population. If they had ever reunited, the two populations probably would have been incapable of interbreeding and producing viable offspring. They developed prezygotic or premating barriers because of habitat isolation and size differences. Even if there is a gene flow between the two populations, strong differential selection may impede assimilation and different species may eventually develop. Terrestrial theropods were generally large, whereas arboreal theropods were small. The arboreal coelurosaurs were the founder population that led to the origin of birds and the evolution of flight. With such a small gene pool, rare genes were passed down more often, which caused genetic drift. The niche partitioning led to a drastic loss of genetic diversity, which, combined with genetic drift, ensured reproductive isolation from the original population. Genetic drift causes loss of alleles. Because drift is a random process, it is likely that each population lost different alleles, making them steadily more different. Natural selection caused the populations to adapt to their environments. As these environments were different, the adaptations of the populations were different. The critical factor in evolutionary change is reproductive isolation because it obviously stops interbreeding. In a small isolated arboreal population of coelurosaurs, when genetic mutations occurred, the features related to arboreal adaptations such as long arms, swivel wrist joints, a stiff tail, and feather integuments were rapidly perpetuated and modified for flight adaptations.

Stomach contents suggest different food preferences between terrestrial and arboreal forms (see chapter 15). Among seed-eaters, terrestrial theropods probably fed on harder seeds from the ground than did arboreal birds, which subsisted on soft seeds. Similarly, terrestrial predatory theropods preyed on larger prey species, while arboreal forms relied on insects and small prey available in trees.

Bird evolution is much more complex than that of arboreal primates because of recurrent flightlessness and reversal of habitats. The large terrestrial theropods in each successive clade of coelurosaurs such as maniraptorans, paravians, and eumaniraptorans may represent flightless forms as Paul (2002) has suggested. As these arboreal forms reverted to terrestrial forms, they became larger and larger. This is why some large maniraptorans retained traits such as encephalized skulls, elongated forelimbs, and powerful shoulder girdles, which might have been acquired by their arboreal ancestors. Vertical niche partitioning between terrestrial and arboreal theropods might be the prime stimulus for the evolution of birds.

4 *Archaeopteryx*: An Ancient Wing

A free bird leaps on the back of the wind
And floats downstream till the current ends
And dips his wings in the orange suns and dares to claim the sky.

Maya Angelou, *I Know Why the Caged Bird Sings*, 1969

The Jurassic World

During the Late Jurassic period (about 160 million years ago), Pangea began to rift apart, opening the Atlantic Ocean from north to south, leaving great deposits of evaporites along the Gulf of Mexico. Laurasia began to separate from Gondwana, forming much of the coastline bordering the Tethys Sea north of the equatorial belt (fig. 4.1). Climates became warm worldwide, and moist winds from newly created oceans brought rain to the continental interior, supporting lush vegetation (cycads and conifers). Dinosaurs became giants, spread throughout the Jurassic world, and adapted to a wide range of environments from the equator to the polar regions. Above the heads of dinosaurs small birds and pterosaurs flew in the Jurassic sky. The plesiosaurs and ichthyosaurs dominated the shallow seas along with crocodilians and turtles and myriads of invertebrates to become the top carnivores in the marine food chain.

Bird skeletons from the Jurassic world are relatively rare. The most celebrated fossil is *Archaeopteryx lithographica* from the Late Jurassic Solnhofen Limestone of Germany. Several bird-like feathered paravians such as *Xiaotingia*, *Anchiornis*, and *Aurornis* from the Late Jurassic of China have been described recently that shook the pivotal position of *Archaeopteryx* in bird phylogeny (Xu et al. 2011; Godefroit et al. 2013a, 2013b). A tantalizing bird skeleton with feather impressions has been discovered in Korea but awaits description and diagnosis (fig. 4.1). Various avialan footprints from North America and Africa indicate that birds were more diverse during the Jurassic than is generally believed.

Archaeopteryx of Altmühl

Until recently, our knowledge of the origin of birds and the evolution of flight was based entirely on *Archaeopteryx lithographica* from the Upper Jurassic Solnhofen Limestone of Germany. This fine-grained limestone, which is extensively quarried for lithographic stone, was deposited in a shallow lagoon of the tropical Tethys Sea. *Archaeopteryx* has been held as the crown jewel in paleontology since the beginning of Darwinian evolution. The story of *Archaeopteryx* begins in 1860 with the discovery of the impression of

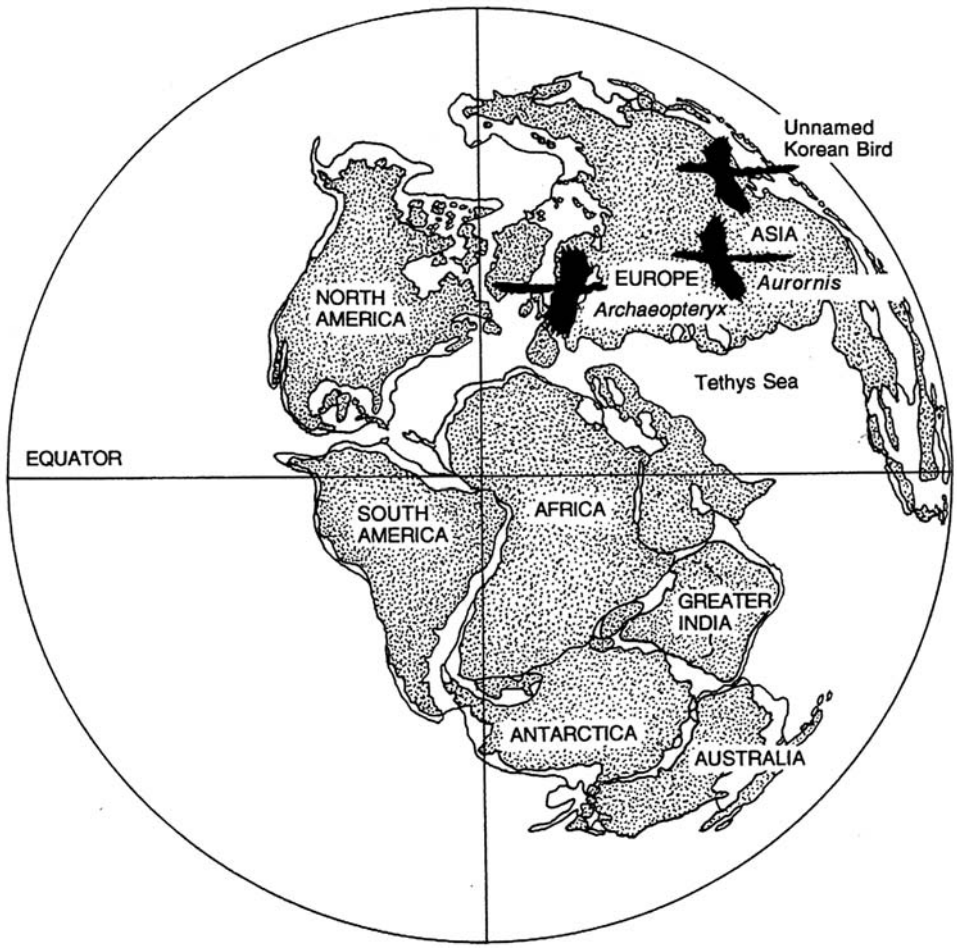


Figure 4.1. Late Jurassic continental configuration showing the location of *Archaeopteryx* from Germany; other controversial birds such as *Xiaotingia*, *Aurornis*, and *Anchiornis* from Liaoning Province of China; and an undescribed Korean bird featured in a Japanese pictorial magazine and dubbed by President Kim II Sung of North Korea as "*Proornis coreae*" (modified from Chatterjee 1997).

an isolated feather in the pastoral Altmühl Valley, near the town of Solnhofen, not far from Munich (fig. 4.2A). The feather was 60 millimeters long and 11 millimeters wide; it was asymmetrical, with two unequal vanes separated by a central shaft, or rachis. The specimen was reported in 1861 by the German paleontologist Hermann von Meyer (1861a). One month later, von Meyer (1861b) reported the discovery of a second specimen from the same Solnhofen limestone, an almost complete skeleton associated with distinct feather impressions. He recognized a curious admixture of both reptilian and avian features in the skeleton and coined a neutral name to designate this specimen, *Archaeopteryx lithographica*, which means "ancient wing from the lithographic limestone." Two years later this specimen was sold to the Museum of Natural History of London for 700 British pounds. The London specimen (fig. 4.2C) includes almost the entire skeleton. The skull bones are scattered but preserve a natural endocast. The specimen was described in detail by Sir Richard Owen (1863) of the British Museum of Natural History as an aberrant bird without any evolutionary implications. Thomas Huxley (1868a, 1868b), on the other hand, emphasized the importance of *Archaeopteryx* as a transitional form between reptiles and birds. The reptilian features include teeth, a long bony tail, gastralia, and sharp claws in the wings. The avian characteristics are feathers,

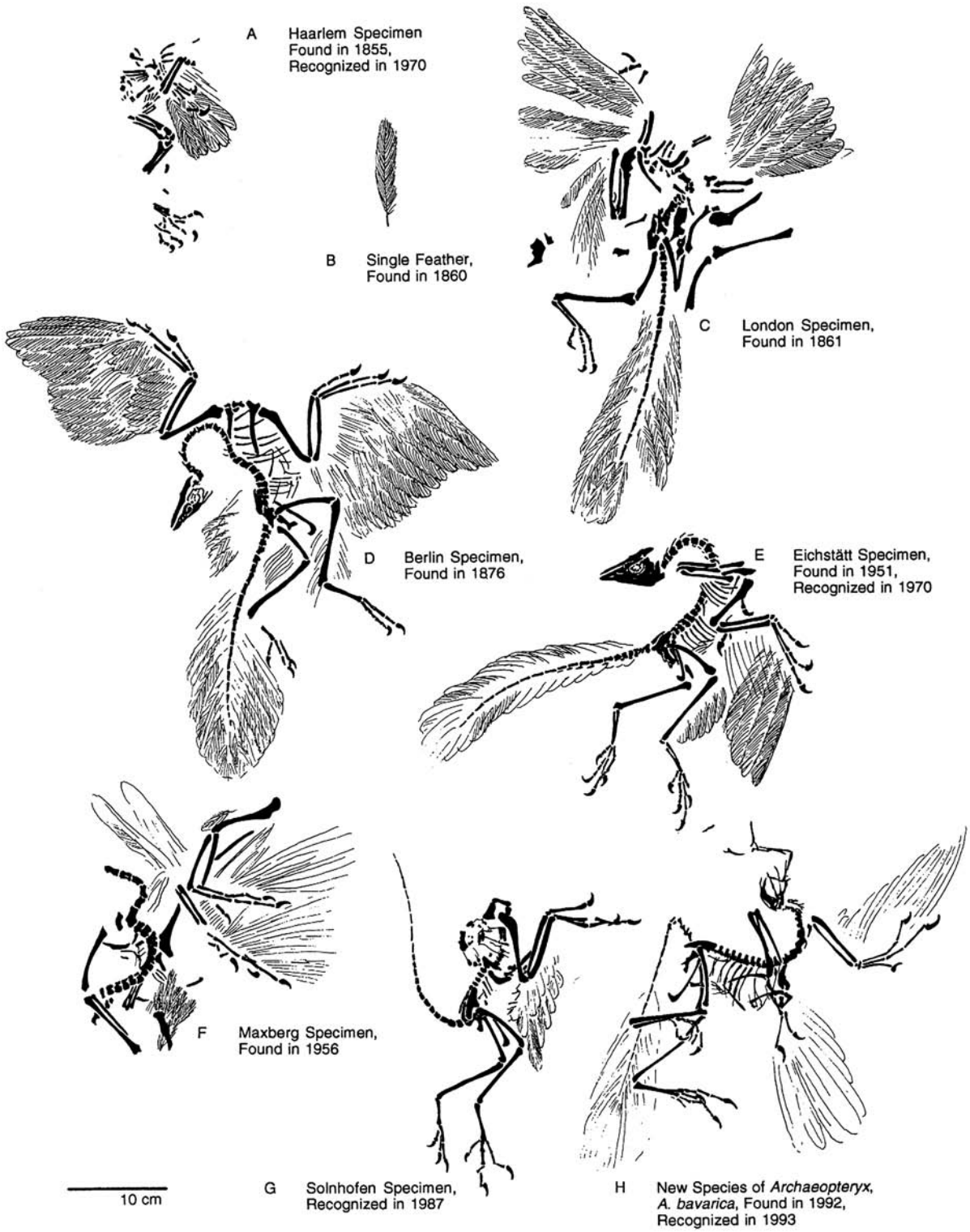


Figure 4.2. Seven fossil skeletons and a solitary feather of *Archaeopteryx,* including the popular name and the year of discovery or recognition (after Chatterjee 1997). In recent times, three more specimens of *Archaeopteryx* have been added to the list, bringing the total number of specimens in existence to eleven.

a furcula, and a reverted pubis. Surprisingly, Huxley used *Compsognathus*, not *Archaeopteryx*, as a missing link between dinosaurs and birds. He viewed *Archaeopteryx* as a side branch of the main line of bird evolution, having little to do with the origin of modern flying birds. He considered *Archaeopteryx* somewhat irrelevant to the issue of bird origins. Although *Archaeopteryx* was the first fossil to support Darwin's theory of evolution, which had been published only two years earlier, Darwin remained almost silent regarding *Archaeopteryx* and never used it in defense of his theory.

The third specimen of *Archaeopteryx* was reported by E. Häberlein in 1877 and is now housed at Berlin's Humboldt Museum of Natural History. The Berlin specimen (fig. 4.2D) is by far the best; the skeleton is articulated in a natural pose with an intact skull and extended wings. The fossil was exquisitely preserved, including the fine structural details of feathers on its wings and tail.

This was the beginning of a series of discoveries of *Archaeopteryx* specimens from the Solnhofen Limestone that would captivate paleontologists and evolutionists for more than a century. The specimens are identified on the basis of the institution that either originally or presently houses them. These are known as the London, Berlin, Eichstätt, Solnhofen, Maxberg, and Haarlem specimens, respectively (fig. 4.2). The Solnhofen specimen (fig. 4.2G) is by far the largest; it was named *Wellnhoferia grandis* by the Polish paleontologist Andrzej Elzanowski in 2001. Peter Wellnhofer (1993) described the smallest of the specimens; it shows two features unknown in other skeletons: an ossified sternum and interdental plates on the inner side of the lower jaw. Wellnhofer concluded that it was an adult specimen representing a new species, *Archaeopteryx bavarica* (fig. 4.2H). In 2004, an isolated right wing of an *Archaeopteryx* was recovered from a quarry near Solnhofen, which is currently on display at Bürgermeister-Müller Natural History Museum in Solnhofen, Germany. Mayr et al. (2005) described another beautiful specimen of *Archaeopteryx*, called the Thermopolis specimen (named after Thermopolis, Wyoming, where it is now housed), with complete head and feet. In 2011, another exquisite postcranial specimen of *Archaeopteryx* was found in the Solnhofen Limestone with intact feather impressions.

The taxonomy of *Archaeopteryx* has been controversial since its first discovery even though to date only eleven skeletal specimens and one isolated feather have been referred to the genus. Over the years, different specimens have often been assigned to different taxa, including *Archaeornis*, *Griphosaurus*, *Griphornis*, *Jurapteryx*, and *Wellnhoferia* on the basis of minor or subjective differences. Part of the confusion surrounding the taxonomy of *Archaeopteryx* may result from the size differences between the specimens of *Archaeopteryx*, which represent growth stages of a single species, *Archaeopteryx lithographica*. Luis Chiappe, who has studied hundreds of Chinese avialan specimens of *Confuciusornis*, found similar morphological variations in the population because of sex and growth; he concluded in his 2007 book, *Glorified Dinosaurs*, that all known specimens of *Archaeopteryx* were members of the same species, *Archaeopteryx lithographica*.

Debate continues about two primary alternative definitions and placements for the taxon name of living and fossil birds: Avialae versus Aves. Gauthier (1986) established the term "Avialae" ("bird wings") to encompass *Archaeopteryx* plus ornithurine birds. Gauthier also proposed restriction of the term "Aves" to crown group birds, that is, living taxa of birds and all the descendants of their most common ancestor. Throughout this book, I use the clade name "Avialae" for *Archaeopteryx* and most basal birds and reserve the name "Aves" for modern birds.

The Great *Archaeopteryx* Debates

The avialan identity of *Archaeopteryx* has been debated for almost 150 years. Controversy started immediately as J. Andreas Wagner (1862) of the University of Munich, who had previously described the splendid specimen of *Compsognathus* from the same limestone strata, proclaimed that *Archaeopteryx* was not a bird but a feathered reptile. He substituted a new name for it, *Griphosaurus problematicus*, with a reptilian emphasis, relating the new specimen to the fabulous griffin lizard.

It is ironic that Charles Darwin in later editions of his *On the Origin of Species* never embraced *Archaeopteryx* as a transitional form between reptiles and birds to bolster his theory of evolution, although his "bulldog," Thomas Huxley, cited *Archaeopteryx* as an evolutionary

link between theropods and birds (Huxley 1868b, 1870). Instead, Darwin was impressed with the evolutionary significance of the Cretaceous birds of Kansas such as *Ichthyornis* and *Hesperornis*. Did Darwin suspect the bird identity of *Archaeopteryx*, or did he want to avoid controversy with his archenemy, Richard Owen, who described the London *Archaeopteryx*? We may never know why Darwin was reluctant to cite *Archaeopteryx* as a centerpiece in support of his theory of evolution.

Archaeopteryx is widely accepted as being the most basal bird, an evolutionary link between theropods and early birds, but there were always dissenters. Ostrom (1976a) concluded that the skeleton of the primitive bird *Archaeopteryx* is virtually identical to that of coelurosaurs with the exception of a furcula and unique ischial morphology. *Archaeopteryx* was insulated with feathers for endothermy and learning to fly from the ground up. Ostrom's student, Robert Bakker (1986), argued that *Archaeopteryx*, in spite of its bird-like appearance, was an earthbound theropod and could not fly. Martin (1985) and Charig (1985) were more cautious about the phylogenetic significance of *Archaeopteryx*. They suggested that *Archaeopteryx* was not an ancestral bird and was far off from the main line of avian evolution. Others argued that *Archaeopteryx* was a feathered dinosaur, not a bird (Lowe 1935; Thulborn 1984; Kurzanov 1985). More recently, Greg Paul (1988, 2002) incorporated *Archaeopteryx* as a dromaeosaur, thus moving the iconic bird well outside the avialans back to the maniraptoran theropods. Wellnhofer (2004) concluded that the skeleton of *Archaeopteryx* had a coelurosaurian bauplan like its sympatric genus *Compsognathus*. Ironically, the lack of fossils similar to the body plan of *Archaeopteryx* made its Urvogel position secure and safe for 150 years.

The skeleton of *Archaeopteryx* is a mosaic of paravian and early avialan characters, representing a clear example of evolutionary experimentation toward the avialan body plan. There are many skeletal features that *Archaeopteryx* inherited from its paravian ancestors, and they are quite archaic compared to those of modern birds. Thus the definition of basal birds is somewhat arbitrary, based on the unique characters of *Archaeopteryx* that separate it from its closest paravian relatives. Traditionally, *Archaeopteryx* had always been regarded as the basal bird because of the presence of feather impressions that resemble those of modern birds. The feathers have a central shaft and asymmetrical vanes formed by hundreds of parallel barbs; there is a similar number of primary and secondary feathers. The wing lacks the alula, however. The discovery of scores of feathered coelurosaurs from the Middle-Late Jurassic and Early Cretaceous of China rekindled the long disputed question of whether *Archaeopteryx* was an avialan or just another feathered theropod (Wellnhofer 2004; Xu et al. 2011). Since similar asymmetric feathers are now known in nonavian dromaeosaurs such as *Microraptor*, they can no longer be used to define the avian status of *Archaeopteryx*. For fossils, we need osteological characters to identify a bird. In this respect, the skeleton of *Archaeopteryx* is exceedingly similar to that of dromaeosaurs, as Ostrom (1976a) has documented, except probably for the innovation of a perching foot (the first toe has rotated backward) and a few other characters.

For more than 150 years, *Archaeopteryx* was iconic in paleontology as the most primitive and the oldest bird, from which all other birds could be derived. It stood practically alone and unchallenged, revered as the Urvogel, the first bird and a symbol of evolution in textbooks. Yet in recent years, the presumed avian features of *Archaeopteryx*, including highly elongated, robust forelimbs, swivel wrist joints, three-fingered hands, a wishbone, asymmetric flight feathers, and snout mobility, were identified in numerous small feathery maniraptoran theropods, thus indicating that *Archaeopteryx* is not a true bird. The once sharp line between paravian theropods and early birds has become murkier in recent years as new, feathered fossils have surfaced in China.

A Team of Rivals to *Archaeopteryx*

It is ironic that for nearly 150 years, *Archaeopteryx* enjoyed the iconic position of Urvogel because there was no rival to challenge its venerated position in evolutionary history. With the discovery of scores of exquisite feathered paravians and avialans from the Middle-Late Jurassic and Early Cretaceous of China during the past decade, *Archaeopteryx* has become just one of several contenders for the status of most primitive bird among a big crowd of feathered paravians. The novelty of *Archaeopteryx* has gone

forever. *Archaeopteryx* has to compete with these Chinese newcomers to regain its past glory. Time will tell whether *Archaeopteryx* is still a bird or actually belongs in a sideline of deinonychosaurs.

The taxonomic status of *Archaeopteryx* at present is in a fluid state, moving back and forth between deinonychosaurs and basal avialans with discoveries of more and more bird-like fossils from the Middle-Late Jurassic Tiaojishan Formation of northeastern China such as *Xiaotingia*, *Anchiornis*, and *Aurornis* that lived side by side at the same time in the same place. This treasure trove of fossils from China shakes the evolutionary tree of early birds and makes the avialan status of *Archaeopteryx* unstable. Many of the deinonychosaurs are known to have possessed bird-like traits such swivel wrist joints, large wings with asymmetric flight feathers, wishbones, and sternums. But certain finer points of the family tree remain debated, with vigorous discussion over the exact position of *Archaeopteryx*. While traditionally considered a basal member of Avialae (Gauthier 1986; Turner et al. 2012), some recent studies find that *Archaeopteryx* branched off before the deinonychosaurian-avialan split (Mayr et al. 2005)—a hypothesis previously suggested by Paul (1988, 2002)—or was a basal member of Deinonychosauria (Xu et al. 2011; Godefroit et al. 2013a). The interrelationships of paravians are not secure at this moment and there will be constant changes in the phylogenetic position of *Archaeopteryx* with the discovery of additional feathered eumaniraptorans from China. For the first time, *Archaeopteryx* is facing serious challenges to retaining its glory from contemporary Chinese cousins such as *Xiaotingia*, *Anchiornis*, and *Aurornis*.

A severe blow tarnishing the avialan pedigree of *Archaeopteryx* came from the recent discovery of *Xiaotingia zhengi* from the Late Jurassic Tiaojishan Formation of western Liaoning, China. *Xiaotingia zhengi* is a chicken-sized maniraptoran virtually identical to *Archaeopteryx* (Xu et al. 2011). When details of the anatomy of *Xiaotingia* and *Archaeopteryx* along with data from other maniraptorans and early birds were subjected to rigorous cladistic analysis, the position of *Archaeopteryx* dramatically shifted to that of a deinonychosaurian theropod (fig. 4.3). As a result, *Archaeopteryx* is no longer nested within avialans; according to Chinese paleontologists, it had not achieved the avialan level of organization. In this new realignment, *Archaeopteryx* clusters not only with *Xiaotingia* but also with another Chinese theropod, *Anchiornis*, in the family Archaeopterygidae, which has been removed from avialans and placed in the lineage of deinonychosaurs. In other words, *Archaeopteryx* is no longer a bird and its centrality in the origin of birds may be a moot point. Witmer (2011, 459), while commenting on the significance of *Xiaotingia*, summarized the flip-flopping status of *Archaeopteryx* and its recent exclusion from the family tree of birds in a memorable line: "Perhaps the time has come to finally accept that *Archaeopteryx* was just another small, feathered, bird-like theropod fluttering around in the Jurassic."

Xu et al. (2011) acknowledged that their conclusions dethroning *Archaeopteryx* from its perch are weakly supported by the available data, highlighting the hazy boundary between avialans and paravians, leading to several species flipping between groups. The basal avialan position of *Archaeopteryx* was restored in a follow-up statistical analysis (Lee and Worthy 2012), but other researchers are seriously questioning the avialan identity of *Archaeopteryx* and support its deinonychosaurian status (Godefroit et al. 2013a). Some have placed *Archaeopteryx* within Avialae on the basis of rigorous phylogenetic analysis (Turner et al. 2012).

Eosinopteryx brevipanna is a small troodontid, about 30 centimeters long, which is known from a single specimen from the mid-Late Jurassic Tiaojishan Formation of the western Liaoning Province of China (Godefroit et al. 2013a). Initially, Godefroit et al. identified it as a basal troodontid along with *Xiaotingia* and *Anchiornis*, but later they grouped it with other scansoriopterygids as a basal member of paravians (Godefroit et al. 2013b). *Eosinopteryx* lived in a swampy environment with plenty of tree cover. The snout of *Eosinopteryx* is abbreviated, shorter than the diameter of the orbit. This flightless form had a small wingspan but retained contour feathers. Unlike its contemporaries *Anchiornis* and *Xiaotingia* from the same horizon, *Eosinopteryx* lacked long contour feathers on its feet and tail, and its toe claws are less recurved, suggest-

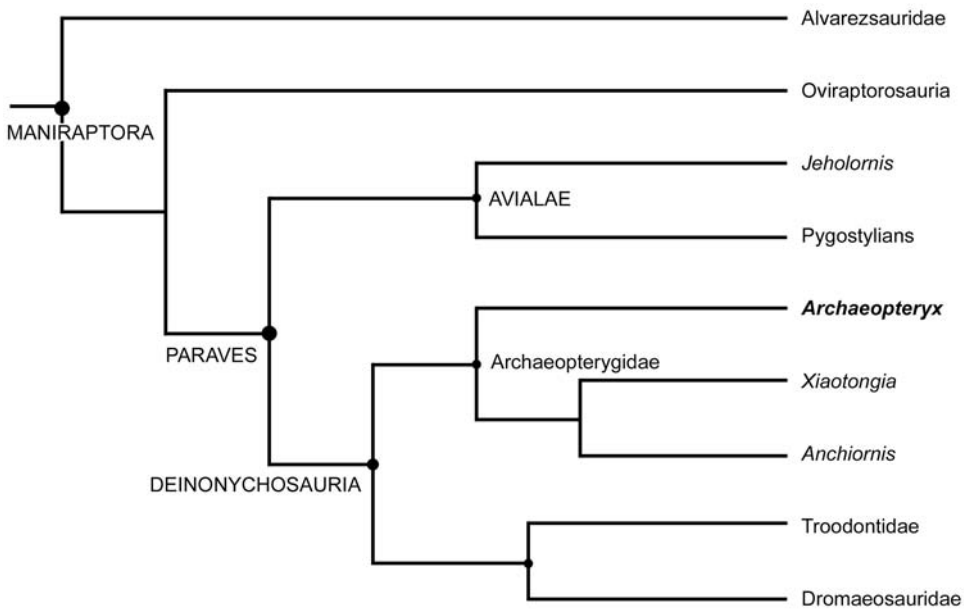


Figure 4.3. Phylogenetic relationships of Paraves with the changing position of *Archaeopteryx* in the avialan tree. Inclusion of two closely related paravian taxa from the Late Jurassic of China, *Xiaotingia* and *Anchiornis*, pulls *Archaeopteryx* out of the avialan clade and puts it into deinonychosaurs along with dromaeosaurids and troodontids. In this phylogenetic realignment, oviraptorosaurs become the close sister groups of avialans. *Jeholornis* is designated as the most primitive, generalized bird fossil from which other birds could be derived. In this new realignment, *Archaeopteryx* is no longer a bird (Avialae) but a member of deinonychosaurs (simplified from Xu et al. 2011).

ing that it could walk and run on the ground. The inclusion of *Eosinopteryx* in the cladogram removed *Archaeopteryx* from the avialan clade.

However, the nonavialan status of *Archaeopteryx* was short-lived. In a subsequent paper Godefroit et al. (2013b) reported the discovery of another chicken-sized flightless bird, *Aurornis xui*, from the Middle-Late Jurassic Tiaojishan Formation of China that has restored the avialan identity of *Archaeopteryx* (fig. 4.4). The single specimen of *Aurornis* is beautifully preserved in two dimensions with every bone in its natural position; traces of downy feathers appear along the animal's tail, chest, and neck (fig. 4.5C). The animal would be about half a meter long from the tip of its beak to the end of its tail; many of its features are similar to those of *Anchiornis*. The skull has small teeth throughout the jaws, and the diapsid arch appears to be intact. The absence of large contour feathers suggests that *Aurornis* could not fly and probably became secondarily flightless. The fossil was purchased from a local fossil dealer and was housed in a local Chinese museum, so its provenance remains uncertain. Most likely it came from the Tiaojishan Formation, which has shale beds similar to the matrix that surrounds the fossil. The team was able to do a detailed cladistic analysis of a large number of paravian taxa employing large datasets that put *Archaeopteryx* back into the avialan lineage along with *Anchiornis*, *Xiaotingia*, and *Aurornis*. In this new analysis, *Epidendrosaurus* and *Epidexipteryx* were removed from Avialae and placed with the basal-most paravians as a sister group of Eumaniraptora, whereas troodontids become the closest sister group of avialans (fig. 4.4). The new phylogeny supports a single origin of powered flight and shows that basal avialans were highly diversified in Eurasia during the Middle-Late Jurassic. The implication of the Jurassic diversity of avialans is that the origin of birds must have occurred much earlier, perhaps in the Triassic. *Aurornis* lived about 150 million years ago, much earlier than *Archaeopteryx*, and has been dubbed the first bird (Godefroit et al. 2013b).

Not everyone agrees with the interpretation of *Au-*

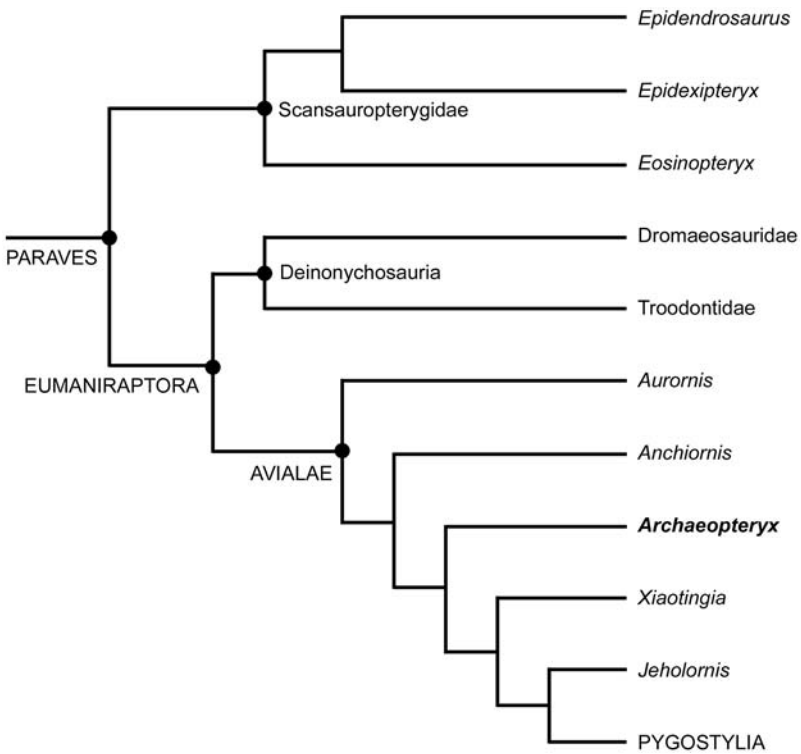


Figure 4.4. New phylogenetic relationships of Paraves. The bird-like *Aurornis* from the Late Jurassic of China restores the avialan status of *Archaeopteryx* along with *Anchiornis* and *Xiaotingia* (simplified from Godefroit et al. 2013b). However, *Xiaotingia* and *Anchiornis* may represent the basal members of troodontids (Turner et al. 2012).

rornis because the flattened fossil is difficult to interpret and its provenance remains uncertain. It is not preserved well enough to discriminate enough anatomical details unequivocally. The analysis of the specimen and its place in the evolutionary tree are up for discussion. Most researchers agree that *Aurornis* is very bird-like, but that it is not yet a bird. For example, the fossil's forelimb is much shorter than that of true birds, whereas the bony tail is more elongated like that of paravians. Moreover, the specimen came from a fossil dealer and its authenticity and provenance are suspect. Godefroit et al. (2013b) considered the possibility that the *Aurornis* fossil might be a fake in supplementary information published to accompany the main paper, but accepted the fossil dealer's claim that it was found near a site where a specimen of *Anchiornis* was also discovered. The authors acknowledged the possibility that specimen may be 35 million years younger than reported and might have come from the Early Cretaceous Jehol Group. Some researchers claim that the fossil of *Aurornis* is so exquisite that it might be a composite of several specimens, as happened in the forgery of another infamous Chinese paravian, *Archaeoraptor*, in 1999. Whatever its status, *Aurornis* restored the position of *Archaeopteryx* at the base of the avialan tree. Although current debate continues, there are two primary alternative placements for *Archaeopteryx*: avialan or deinonychosaur. Until the issue is resolved, *Archaeopteryx* is considered here in the traditional sense that it is a basal member of avialans, with or without help from *Aurornis*.

The phylogenetic positions of basal avialans are changing rapidly as new discoveries provide novel data for phylogenetic analyses. Three controversial basal paravians from the Middle-Late Jurassic of China—*Xiaotingia, Anchiornis*, and *Aurornis*—have profound implications for the phylogenetic position of *Archaeopteryx* in the avialan clade (fig. 4.5). Turner et al. (2012) placed *Xiaotingia* and *Anchiornis* as basal members of troodontids. I suspect that *Aurornis* is closely related to *Anchiornis*. All these ani-

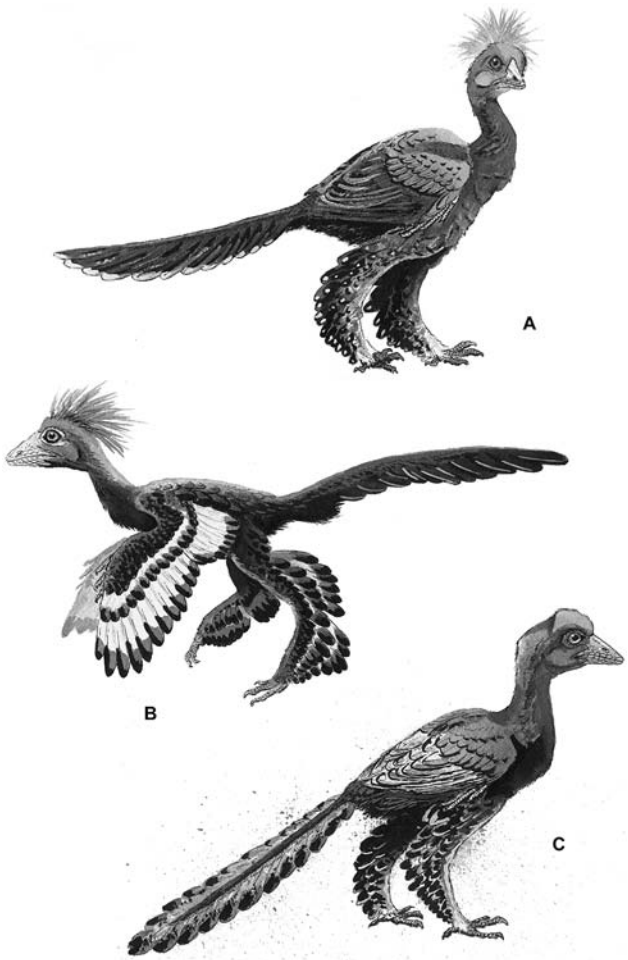


Figure 4.5. Life restoration of three controversial paravians from the Late Jurassic Tiaojishan Formation of western Liaoning Province of China that have reshuffled the phylogenetic position of *Archaeopteryx* in the avialan tree. These three taxa play an important role in understanding paravian and avialan phylogeny. A, *Xiaotingia zhengi*; B, *Anchiornis huxleyi*; and C, *Aurornis xui*.

mals—*Xiaotingia, Anchiornis*, and *Aurornis*—are so similar and there is so much homoplasy that their phylogenetic positions fluctuate from deinonychosaurs to avialans, depending on the choice of characters for phylogenetic analysis.

As discussed in the previous chapter, Agnolin and Novas (2013) and I regard these four-winged tetrapterygids—*Microraptor*, *Xiaotingia, Anchiornis*, and *Aurornis*—as a close sister group of Avialae; tetrapterygids and avialans, in turn, are accommodated in a larger clade, Averaptora. Instead of two wings, tetrapterygids had four wings in biplane configuration (Chatterjee and Templin 2007a). Two-winged flight with a monoplane wing planform followed the emergence of *Archaeopteryx* and other avialans, although some species such as *Sapeornis* retained the primitive four-winged configuration (see chapter 12). It is amazing that so many early birds and their immediate ancestors had large leg feathers.

Scansoriopterygids have been classified as avialans along with *Jeholornis* (Xu et al. 2011), but their secondary loss of flight and reversal of some anatomical characters make their avialan status somewhat shaky. They are now regarded as basal groups of paravians (Godefroit et al. 2013b). In spite of all the recent taxonomic turmoil, *Archaeopteryx* is considered here as an early avialan until its phylogenetic position is fully resolved (fig. 4.6).

The question of basal avialan relationships cannot be answered properly until good candidates for the long-tailed ancestry of all pygostylian birds such as *Sapeornis* and *Confuciusornis* are identified. *Jeholronis* from the Early

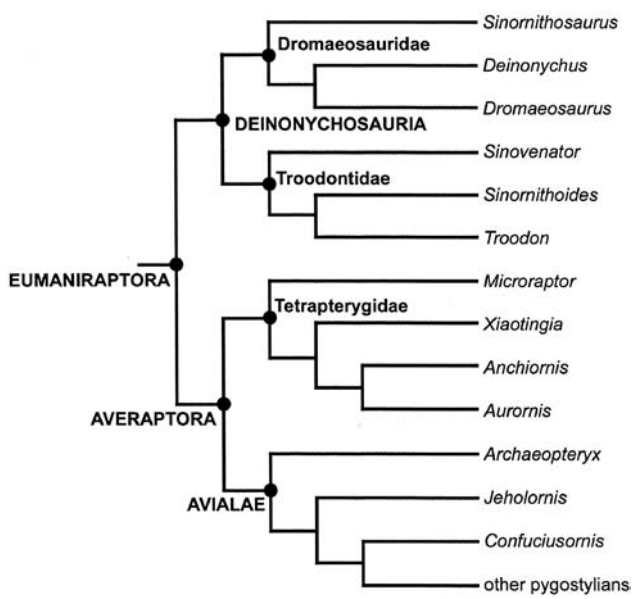


Figure 4.6. Cladogram depicting the interrelationships of major groups of eumaniraptorans adopted in this book. *Archaeopteryx* is placed here in the traditional sense as the most basal member of Avialae. However, *Jeholornis* appears to be a better candidate for the stem group of avialans than *Archaeopteryx* and its phylogenetic position is more stable and secure.

Cretaceous of China is more derived and a better flier than *Archaeopteryx* with the development of a fused carpometacarpus, a scapula with a dorsolaterally exposed glenoid facet, and a large sternum. *Jeholornis* seems to be the right candidate to represent the new Urvogel rather than the controversial *Archaeopteryx*.

The Anatomy of *Archaeopteryx*

In spite of the excellent preservation of several skeletons, detailed anatomical information on *Archaeopteryx* is still lacking. The main reason for this deficiency is that none of the specimens has been completely prepared and freed from the limestone matrix (Martin 1995a). Our knowledge of the anatomy of *Archaeopteryx* is thus limited to its two-dimensional profile. The skull of *Archaeopteryx* is difficult to interpret because of extensive crushing. Peter Wellnhofer, a leading authority on *Archaeopteryx*, made the first accurate restoration of the Eichstätt skull in 1974. Alick Walker (1985) provided a detailed interpretation of the braincase of the London specimen. Later, I modified the skull restoration on the basis of additional evidence gleaned from the London and Berlin specimens. The seventh specimen, often mentioned as *Archaeopteryx bavarica*, provides additional cranial information (Elzanowski and Wellnhofer 1996).

Archaeopteryx is a medium-sized bird, 30 to 50 centimeters long from the tip of its snout to the end of its tail; adult individuals weigh about 600 grams, approaching the size of a common crow. The skull of *Archaeopteryx* is dromaeosaur-like in general structure. It retains many primitive features, such as interdental plates, an ectopterygoid, an epipterygoid, the rostroventral wing of the prootic, postorbital-squamosal processes, the ascending process of the jugal, and distinct sutures (fig. 4.7A). Numerous carnivorous teeth are present in the rostral half of the jaws, and these teeth continue at the midpoint of the antorbital fenestra. The teeth are conical, unserrated, and widely spaced, with distinct necks and replacement pits; they are bordered by a series of inderdental plates at the lingual margin. The nasal opening is large and elliptical, and the maxilla takes part in the formation of the rim, as in primitive archosaurs. The antorbital opening is triangular and has two internal foramina in front of it. The nasal bones act as median roofing elements between the premaxillae and the frontal bones. The frontals show inflated topography for housing of the cerebrum. The parietals have a median crest. The orbit is large and circular, containing a ring of sclerotic plates, and is somewhat laterally placed. There is a partial modification of the temporal region. The postorbital is present, but the ascending process of the jugal seems to be reduced in the juvenile Eichstätt specimen but complete in the adult London specimen. Because of this change, the lower temporal opening communicates with the orbit in the juvenile individual, while the upper temporal arcade remains intact (fig. 4.7A).

The squamosal-quadratojugal bar appears to be present in front of the quadrate, but their connection is probably lost, as seen in ceratosaurs. This bar would act as a blocking device to prevent streptostylic movement of the quadrate. The quadratojugal is L-shaped and makes a long sutural contact with the quadrate. The palate is poorly known, but it retains the ectopterygoid bone. The palatine is bird-like and is differentiated into three flanges: the premaxillary process rostrally, a hook-shaped choanal process, and a long pterygoid wing. The quadrate is very similar to that of a nonavian theropod, with a single head contacting the squamosal and paroccipital process. It bears a large pterygoid flange but lacks the avian orbital process. Its ventral surface shows bicondylar articulation with the lower jaw. The lower jaw is slender and lacks the coronoid and lateral mandibular fenestra. The inflated frontal and modified temporal regions seem to be two avian attributes in the skull roof of *Archaeopteryx*.

The braincase of *Archaeopteryx* is more derived and exhibits many features of primitive birds. It has developed all three tympanic recesses (rostral, dorsal, and caudal) in the same topographic positions as in modern birds (fig 4.7B). The otic capsule shows the fenestra ovalis and fenestra pseudorotunda, separated by a thin crest of opisthotic. The dorsal end of the opisthotic displays a typical concavity leading to the caudal tympanic recess. There is a development of the metotic strut behind the fenestra pseudorotunda so that the vagus canal (cranial nerve X)

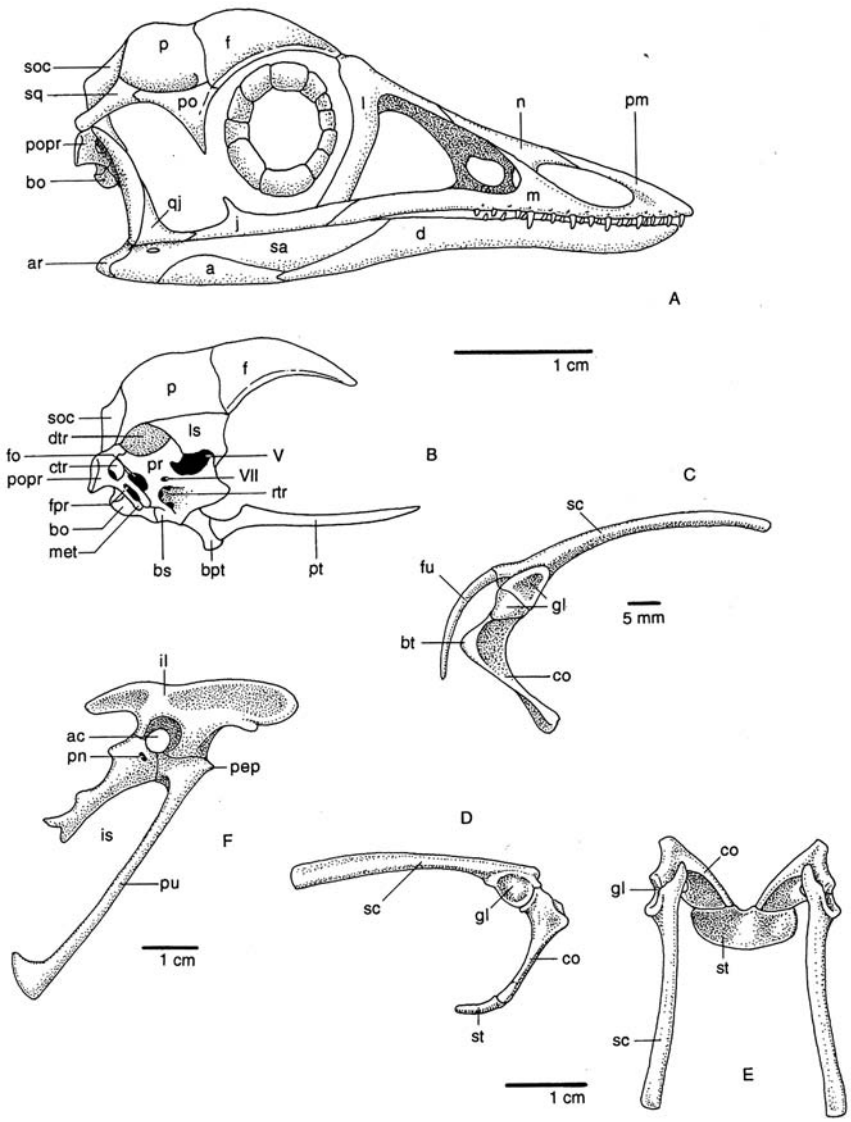


Figure 4.7. Composite restoration of skeletal elements of *Archaeopteryx*. A, reconstruction of the *Archaeopteryx* skull based on the Eichstätt specimen, representing a juvenile individual. The temporal region of the skull is poorly understood; however, the orbit may be confluent with the lower temporal fenestra, a condition also seen in a small alvarezsaurid theropod such as *Shuvuuia* from Mongolia. The incomplete squamosal-jugal arch may indicate a juvenile feature. In an adult individual, represented by the London specimen, the diapsid arch seems to be intact. B, braincase; C, shoulder girdle; D and E, lateral and dorsal views of right shoulder girdle of *Archaeopteryx bavarica*, showing a small, ossified sternum (after Wellnhofer 1993); however, other scientists have questioned the validity of this new species and suggested that the sternum was misidentified. F, pelvic girdle (after Chatterjee 1997). For abbreviations, see figures 5.4–5.9.

has diverted back to the occiput. The occiput shows a sinus canal between the epiotic and supraoccipital. The brain is fairly large, and the encephalization quotient (EQ) is 0.34, which is in the range of some living birds.

John Ostrom (1976a) has shown many similarities in the postcranial skeletons of *Archaeopteryx* and dromaeosaurs. Wellnhofer (1974, 1993) described the postcranial skeleton of *Archaeopteryx* in detail. The neck is long and flexible, and the thorax is comparatively short and compact. The vertebral column is like that of nonavian the-

ropods. There seem to be nine cervical, fourteen dorsal, five sacral, and twenty or twenty-one caudal vertebrae. The centra are amphicoelous throughout the column and lack hypapophyses. Some posterior dorsal vertebrae show small pleurocoels. In the tail region, the zygapophyses are highly elongated and the chevrons behind the seventh caudal vertebra are prominent. The tail is unique, in that it has a row of rectrices on either side. The thoracic ribs lack uncinate processes, and a series of gastralia behind the coracoids are present in all specimens.

The scapulocoracoid (fig. 4.7C) is reminiscent of the condition in dromaeosaurs, in which the scapula is long, slender, and strap-like; the coracoid is subrectangular, with the development of a biceps tubercle below the glenoid. A suture joins these two bones in *Archaeopteryx*, unlike in dromaeosaurs. Moreover, the glenoid has shifted its position from backward to outward. The biceps tubercle—the precursor to the avian acrocoracoid—is more pronounced in *Archaeopteryx* and projects forward. However, the coracoid of *Archaeopteryx* is primitively built. It lacks all of the avian features, such as a strut-like configuration, a procoracoid, an acrocoracoid, and a triosseal canal. In modern birds, the pulley-like action of the triosseal canal allows the suparcoracoideus muscle to elevate the wings. The absence of a triosseal canal in *Archaeopteryx* indicates that the upstroke during flight was feeble. The development of a strong, robust, U-shaped furcula is the main departure from the dromaeosaurid design (fig. 4.7D–E). The sternum appears to be unossified in all specimens.

The forelimbs were modified as wings. They show long flight feathers extending out from the hand and lower arm bones. The humerus is primitive, with a large deltopectoral crest, but lacks the avian bicipital crest. The two expanded ends lie oblique to each other. The distal condyles and epicondyles are not well differentiated. The radius and ulna are long and slender and display the same proportions as in dromaeosaurs. The tridactyl manus with its hook-like claws is exceptionally large and represents about 40% of the length of the forearm. The wrist has the distinctive semilunate distal carpal, as in dromaeosaurs, to receive metacarpals I and II (Ostrom 1976a). This swivel wrist joint allowed folding of the hand in the plane of the forearm when not in use. The manus is three-fingered: metacarpal I is the shortest, II is the longest, and III is of intermediate size; metacarpals IV and V have been lost. The phalangeal formula is 2-3-4-x-x, and the terminal claws are thin and recurved, indicating adaptation for perching and climbing (Feduccia 1993).

The pelvis is more advanced than in dromaeosaurs. The configuration of the pelvis of *Archaeopteryx,* especially the orientation of the pubis, has generated much controversy in recent years. Ostrom has restored the pelvis in a nonavian, theropod fashion, with the pubis extending vertically, but most paleontologists agree that the pubis has been rotated considerably backward, as is seen in the Berlin specimen. The ilium, ischium, and pubis are separate. The ilium has a large, expanded preacetabular process and a stout pubic peduncle (fig. 4.7F). The ischial morphology is unusual, showing a foramen proximally below the acetabulum and a bifurcation at the distal end, which may indicate a cartilaginous extension. The pubis is twice the length of the ischium. It has a pectineal process proximally and shows a distinct foot at the distal end, as in nonavian theropods. Medially, the pubes are fused at the symphysis.

The hindlimb appears somewhat more advanced than in dromaeosaurs. The femur has an inturned head, well-defined greater and lesser trochanters, a posterior trochanter, and a distal expanded end without any fibular groove. The femoral shaft is somewhat bowed craniocaudally. The tibia, longer than the femur, has a lateral cnemial crest but no cranial crest. The fibula is a thin, splint-like bone and is as long as the tibia. The proximal tarsal elements are not fused with the tibia to form the tibiotarsus. The astragalus has a long and narrow ascending process, and the calcaneum is reduced. The foot is four-toed and anisodactyl. The central toes (metatarsals II, III, and IV) show a partial fusion at the proximal end in the Solnhofen specimen. The phalangeal formula is 2-3-4-5-x; the terminal claws show digital flexors, which may indicate grasping or perching capability. A skeletal restoration of *Archaeopteryx* is shown in figure 4.8.

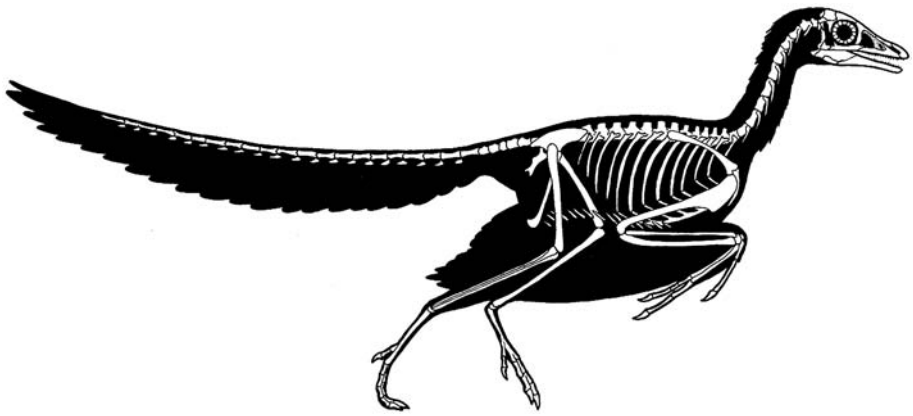


Figure 4.8. Skeletal restoration of *Archaeopteryx*, mainly based on the London specimen.

The Paleoecology of *Archaeopteryx*

What sort of bird was *Archaeopteryx*? What was its habitat? Was it arboreal or cursorial? Could it fly? These are some of the contested issues that have been debated for more than a century. To understand this controversy, we need to know in which paleoenvironment *Archaeopteryx* lived. *Archaeopteryx* lived during the early Tithonian age of the Late Jurassic period, about 150 million years ago. Most of the specimens of *Archaeopteryx* were discovered from the Solnhofen Limestone in Bavaria, southern Germany, which lay at a latitude similar to that of modern Florida, though the climate was much drier. During the Late Jurassic time, Pangea was breaking up; the Tethyan seaway appeared as the northern and southern continental landmasses separated. Arid conditions were accompanied by deposits of evaporites that formed along much of the coastline bordering the Tethys Sea. Animal communities were becoming separated and endemic. The Solnhofen region during this time, as reconstructed by Günter Viohl (1985), was a quiet, tropical lagoon lying behind coral islands on the northern shores of the Tethys Sea (fig. 4.9A). The lagoon was extremely salty and anoxic and did not support life.

Archaeopteryx was obviously an island bird; it evolved in isolation on several Central European Islands, such as the London-Brabant Massif, Central German Swell, and Bohemian Massif. Many of the rich biota from these islands, including cycads, conifers, ginkgoes, insects, lizards, pterosaurs, *Compsognathus*, and *Archaeopteryx*, were probably drowned by occasional storms and carried into this lagoon to be preserved in exquisite detail. The climate was semiarid and tropical, but normally very dry and punctuated at certain times of the year by monsoons sweeping in from the southeast. The adult *Archaeopteryx* was about the size of a raven, about 50 centimeters in length, with toothed jaws, broad wings, and a long bony tail. Recently, the fossilized melanosome pigment from the feather impression of *Archaeopteryx* indicates that it was a black bird like a raven; melanosomes also provided additional strength to abrasion from flight (Carney et al. 2011). *Archaeopteryx* was mostly arboreal, probably perching in ginkgo trees, and fed on insects and small animals; it could glide from tree to tree (Chatterjee and Templin 2003) (fig. 4.9B).

The Solnhofen animals and plants were preserved in the lagoon, far from their original life habitat. The preservation of articulated skeletons of *Archaeopteryx* with feathers as well as contemporaneous pterosaurs with intact skeletal and skin impressions certainly indicate unusual circumstances of fossilization in the Solnhofen setting, perhaps autochthonous burial. The salty lagoon did not support life but was an ideal setting for a mass grave, trapping and preserving an array of island fossils for posterity in exquisite detail. Were the pterosaurs and *Archaeopteryx* downed in flight and blown into the lagoon? Or

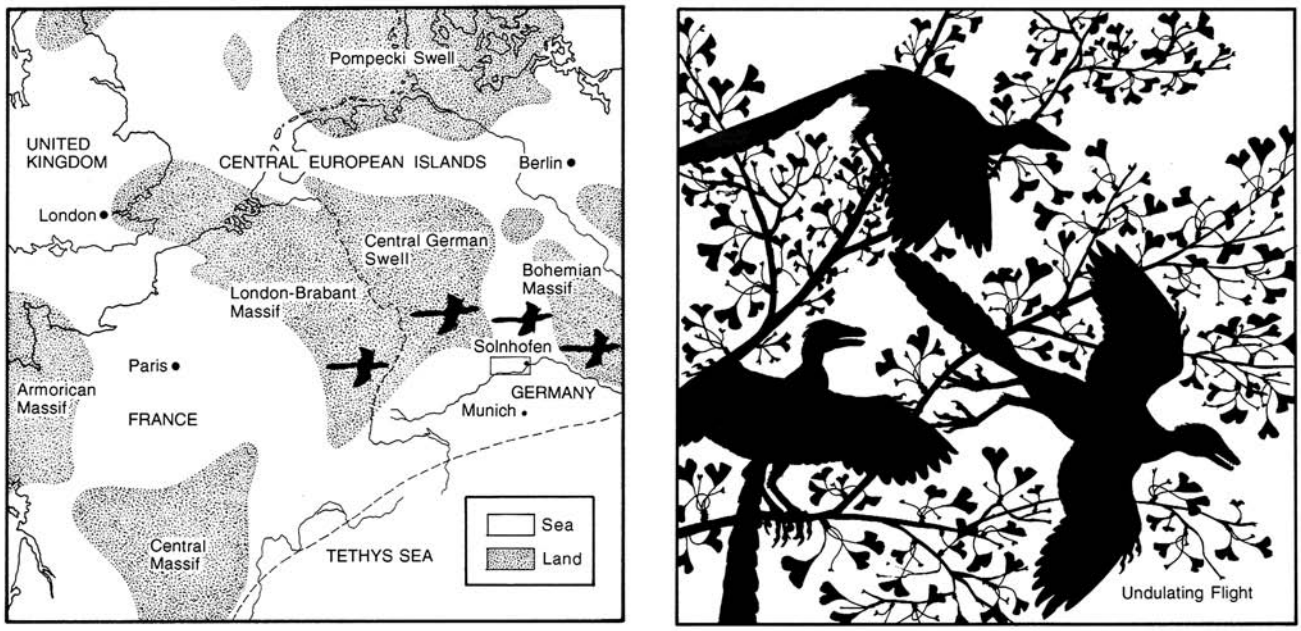


Figure 4.9. A, paleogeography of Central Europe during the Late Jurassic period. The rectangle marks the sedimentation area of the Solnhofen Lithographic Limestone. A shallow sea covered much of Europe. *Archaeopteryx* probably lived in the Central European Islands, such as London-Brabant Massif, Central German Swell, and Bohemian Massif. The animals were probably downed in flight by occasional storms and blown into the Solnhofen lagoon. B, paleoecology of *Archaeopteryx*. Its claw geometry suggests that it was primarily an arboreal and trunk-climbing bird. *Archaeopteryx* was probably capable of undulating flight for a short distance (after Chatterjee 1997).

did they die and become mummified at the beach, then to be transported into deep water, settling eventually into the bottom of the lagoon? These remarkably preserved fossils at Solnhofen evoke many unusual explanations. The water was calm and stagnant; there was no scavenging or bacterial decomposition at the bottom of the lagoon as a consequence of poisonous planktonic bloom. This unusual setting was conducive to the preservation of such delicate, soft structures as feathers, insect wings, wing membranes of pterosaurs, hair-like setae of crustaceans, and medusae of jellyfish. *Archaeopteryx,* a crow-sized bird, lived in the forests of coral islands in Central Europe and was frozen in time into this lithographic limestone by accidental death.

Although traditionally *Archaeopteryx* has been envisioned as an arboreal bird, Ostrom (1973, 1976a, 1985a) suggested that it was a ground-dweller similar to quail and roadrunners. Ostrom was so influenced by the anatomical similarity between *Archaeopteryx* and dromaeosaurs that he interpreted *Archaeopteryx* as a terrestrial cursor without any flying power. He reasoned that it lacks two bony elements that seem to be essential for flight: the ossified, keeled sternum for the attachment of the powerful pectoralis muscle, which executes the downstroke, and a triosseal canal for the supracoracoideus pulley associated with the upstroke. Perhaps *Archaeopteryx* used its feathers to catch insects, Ostrom speculated. Critics such as Larry Martin (1983a) argued that if the wings functioned as insect-catchers in early birds, natural selection would have acted strictly to improve them as flyswatters. In that case avian wings would not have been designed for flight.

Alan Feduccia (1980, 1996) and his colleagues have opposing views about the life habits and flight capability of *Archaeopteryx*. They point out that the shape and arrangement of the primary feathers of *Archaeopteryx* are similar to those of modern flying birds (Feduccia and Tordoff 1979). Each flight feather displays vane asymmetry, in which the smaller vane faces the leading edge. This is an impor-

tant aerodynamic requirement for flight; flightless birds have symmetrical feathers. The sturdy furcula offers other evidence. It provided an expanded site for the attachment of the pectoral muscle, which is used in the downstroke (Olson and Feduccia 1979). The lack of the supracoracoideus pulley may simply indicate that *Archaeopteryx* probably could not take off from the ground. The highly curved claw geometry of both hands and feet and the reversed first toe indicate climbing and perching habits of *Archaeopteryx* (Feduccia 1993). It must have climbed trees and moved between treetops to pursue insects (figure 4.9B). The vegetation in these islands was probably bushland of conifers, seed ferns, ginkgoes, and cycads. A variety of insect fossils, such as cicadas, dragonflies, and wood wasps, have been recorded in the Solnhofen.

Archaeopteryx might also have launched from cliff tops to glide above the beaches and shallow seas for food (Peters 1994). Their sharp, conical teeth, like those of the marine Cretaceous birds *Hesperornis* and *Ichthyornis* and of crocodiles (Martin 1985, 1991), could be used to catch slippery fish. The construction of the pectoral girdle, lack of an ossified sternum and powerful flight muscles, and primitive wrist morphology suggest relatively weak specialization for flapping flight. Although we may never know how well *Archaeopteryx* could fly, the consensus is that it could surely glide and could possibly fly in undulating fashion for a short distance (see chapter 12).

Several features of the brain and inner ear indicate clearly that *Archaeopteryx* was a flying animal (fig. 4.7B). It shows bird-like brain organization with the development of large optic lobes for keen sight, and enlargement of the cerebellum for balance and control. Its brain had developed typical avian architecture and was considerably enlarged from that of nonflying precursors where the estimated encephalization quotient was 0.34 (see chapter 5). Recent computed tomographic x-ray scanning images suggest that *Archaeopteryx* had developed the movement and balance control required for powered flight and not just gliding; this is evident from the tomography of the inner ear with large semicircular canals with a vestibular apparatus, the gyroscope of a flying animal (Alonso et al. 2004). Using a computer simulation model, Chatterjee and Templin (2003) showed that *Archaeopteryx* was a good glider; it was capable of phugoid gliding between trees, but it also appears to have been able to undertake the initial stages of powered flight. However, it lacked muscle power and a supracoracoideus pulley to take off from the ground. Its flapping capability was weak, but it could use undulating flight to save energy.

5 *Protoavis*: A Precocious Triassic Bird

By George, this must be the trail of the father of all birds!

Arthur Conan Doyle, *The Lost World*, 1912

Dawn of the Age of Dinosaurs

The Triassic period of Earth's history, from 251 to 202 million years ago, was an extraordinary time in tetrapod evolution. Several groups of vertebrates such as lissamphibians, turtles, squamates, crocodilians, dinosaurs, birds, and mammals first appeared in the fossil record during this time. The Triassic period began soon after the most catastrophic mass extinction event in geological history at the end of the Permian, when life on Earth was almost completely wiped out by an environmental catastrophe of a magnitude never seen before or since. Only 10% of the species survived this end-Permian extinction that ended the Paleozoic era and heralded the Mesozoic era, thus beginning the age of dinosaurs. More than 95% of marine invertebrates vanished during the Permian extinction. Major victims were immobile and sluggish marine life forms in reef and shallow water communities such as rugose and tabulate corals, trilobites and eurypterids, productid brachiopods, single-celled fusulinids, and many families of bryozoans. The bivalves and gastropods were struck moderately hard. On land, two-thirds of terrestrial vertebrates and nearly one-third of insects disappeared along with the evergreens that formed their habitat. Among land animals, therapsids (ancestors of mammals) were the main victims. Plate movements, mountain building, violent volcanism, and regression of the seas produced major changes in the global distribution of continents and oceans as the Permian drew to a close. The end-Permian extinction is linked to the massive eruptive event of Siberian volcanism that spanned the Permian-Triassic boundary about 250 million years ago and contributed heavily to the breakdown of stable ecological communities and severely disrupted the biosphere. In the aftermath of the biotic crisis, groups of animals that formerly had played minor roles in the ecosystems assumed prominence and new groups appeared. Mass extinction is the game changer of life, destroying the old dynasty and heralding a new age.

There was a dramatic ecological replacement from the Permian to Triassic periods with new casts of life in the Mesozoic scene. During the Late Permian, therapsids—the mammal-like amniotes—dominated the landscape. By the Late Triassic, archosaurs—the ruling reptiles—had replaced therapsids as the leading vertebrates. Most of the therapsids became the victims of the end-Permian catastrophes. During the Triassic, mammals

Figure 5.1. During the Triassic period, all continents formed one supercontinent, known as Pangea. In this Pangean world, the first bird, *Protoavis*, lived in the tropical forests of Texas.

originated from small therapsids, while dinosaurs began to diversify and dominate the landscape. Some little dinosaurs began to explore the air from the tree branches. Pterosaurs, kuehneosaurs, and birds took to the air for the first time and broke the barrier of gravity. Other vertebrates invaded the seas. Lissamphibians, lizards, turtles, and crocodylomorphs also emerged during the Triassic. This faunal turnover in the terrestrial realm revealed the beginnings of many major groups of tetrapods that still persist today. The Triassic was the renaissance in vertebrate evolution in the Pangean world.

The Birth and Breakup of Pangea

The Triassic period was a transition from the Paleozoic era to the Mesozoic. When the Triassic period began, all of the major continental plates were joined into a single colossal supercontinent called Pangea, which was slowly drifting northward (fig. 5.1). Land animals were able to migrate easily back and forth across the land surface of Earth. Pangea comprised two landmasses: Laurasia in the north and Gondwana in the south. The Tethys Sea lay between Gondwana and Laurasia during much of the Mesozoic era, before the opening of the Indian and Atlantic Oceans during the Cretaceous period. What was once the Tethys Sea has become the Mediterranean. Other remnants are the Black, Caspian, and Aral Seas. Today, the Alpine-Himalayan mountain belt marks the relics of the Tethys Sea that was squeezed and folded by continental collision during the Cenozoic.

During the Late Triassic, initial rifting in Pangea began

in the region including eastern North America, southern Europe, and North Africa that marked the early phase in the development of the North Atlantic Ocean. North America began to pull away from Europe and Africa to create rift valleys with the initial formation of the Atlantic Ocean. The sediments that filled these rift valleys are preserved along the eastern margin of North America and the western edges of Africa and Europe and they contain important evidence of the beginning of the age of dinosaurs and their environments. As Pangea began to break apart, regression of the epeiric seas and widespread emergence of continents resulted in deposition of nonmarine red beds in large basins in the interior of the continents around the globe. These red beds were deposited in a complex mosaic of river-deltaic-lake systems in many parts of the world. Today, they are known in India, China, Argentina, Brazil, South Africa, East Africa, Germany, Great Britain, Canada, and the United States. These red beds have yielded a rich record of Triassic vertebrate fauna, including the early dinosaurs. Triassic vertebrates have also been found in Greenland, Australia, and Antarctica.

During this initial fragmentation of Pangea, a rift opened in the southwest Indian Ocean, moving South America and Africa away from Antarctica-Australia. At the same time, the Atlantic Ocean was beginning to open. When the Atlantic opened, huge fractures in the crust of Nova Scotia, New Jersey, and Connecticut served as the conduits for great outpourings of lava. The ancestral Gulf of Mexico began to form farther south. The rifting in the Gulf of Mexico created several intracontinental basins in the American Southwest that became the primary depocenters for the Late Triassic continental red beds of the Chinle and Dockum Group. During the initial stage of rifting, a large meteorite collided with Earth in central Quebec to produce the giant Manicougan crater, about 100 kilometers across (half the size of Connecticut). This was a time of major environmental disruption and biotic crisis. Another mass extinction struck both marine and terrestrial ecosystems at the end of the Triassic. It eliminated a wide range of land vertebrates. Surprisingly, the dinosaurs (including birds) were unscathed, and they proliferated after this crisis to dominate terrestrial habitats (Chatterjee 1992a).

The centralized position of Pangea, straddling the equator, and the tectonic activity associated with its breakup influenced the climate of the Triassic. The continents were of high elevation compared to sea level, and the sea did not invade the coastal areas. The topography and climate became more uniform during the Triassic. The paleoclimate was subtropical, hot and humid, dominated by monsoonal circulation. Provincial biotas developed as well between Northern and Southern Hemispheres. Dense forests and swamps full of conifers, cycads, and ginkgoes covered the northern supercontinent, Laurasia. In contrast, seed ferns, called *Dicroidium*, dominated the southern supercontinent, or Gondwana. By the end of the Triassic, both hemispheres gave way to conifer and cycad vegetation. No ice sheets covered the polar regions during the Triassic.

The Triassic Treasures of Texas

Late Triassic history is represented in West Texas by a richly fossiliferous sequence of continental Dockum sediments. Named by the geologist W. F. Cummins in 1890 after a small town in Dickens County, Texas, these red beds crop out around the Southern High Plains and through the Canadian River Valley in the Texas Panhandle. Strata of the Dockum basin were deposited during the early breakup of the Pangean supercontinent during the Late Triassic time. These strata are important because they contain a record of terrestrial vertebrate life during the initial adaptive radiation of a diverse group of tetrapods, including lissamphibians, turtles, lepidosaurs, trilophosaurs, phytosaurs, aetosaurs, rauisuchians, crocodylomorphs, dinosaurs, pterosaurs, birds, and mammals. These strata can be physically traced and correlated with the Triassic section exposed northwesterly in east-central New Mexico, which probably indicates a contiguous depositional basin. Outcrops of the Dockum Group are best exposed along the escarpment of the High Plains in Texas, and along the western escarpment of the High Plains and Pecos River Valley in New Mexico at the proximity of the

resistant "Caprock" caliche that marks the top of the overlying Tertiary Ogallala Group.

My colleague Thomas Lehman and I have mapped the Dockum rocks in detail and reconstructed their depositional history (Chatterjee 1986; Lehman 1994; Lehman et al. 1992; Lehman and Chatterjee 2005). Triassic strata of the Dockum Group in Texas comprise two major upward-fining alluvial-lacustrine depositional sequences: the Santa Rosa-Tecovas and Trujillo-Bull Canyon Formations (Lucas 1998). The second sequence is much thicker than the first, and occupies a greater geographic part of the Dockum Basin. Currently, Dockum Group strata in Texas are assigned to four formations, in ascending order: Santa Rosa, Tecovas, Trujillo, and Bull Canyon (fig. 5.2). The Tecovas and Bull Canyon Formations consist primarily of red mudstones intercalated with discontinuous, lenticular bodies of sandstones, whereas the Santa Rosa and the Trujillo are dominantly sandstones and conglomerates. The Santa Rosa–Tecovas sequence is separated from the overlying Trujillo–Bull Canyon sequence by an unconformity and by mineralogical change; each sequence generally fines upward and indicates different provenance. The thickness of the Dockum ranges from less than 70 meters to as much as 600 meters; the sedimentation began in the Carnian and continued up to the early part of the Norian. The Dockum Basin, about 400 kilometers wide and 800 kilometers long, was a major depocenter of Triassic sedimentation when the Gulf of Mexico was opening farther south.

The Dockum Group has been an important source of Triassic vertebrate fossils since 1893, when Edward Drinker Cope first recognized the remains of amphibians and reptiles in these red beds. Exposures of the sediments are generally good, and there are numerous outcrops in the tributary valleys of the Brazos, Colorado, and Canadian Rivers. Three bursts of active collecting and research of the Dockum vertebrates occurred during the twentieth century. E. C. Case of the University of Michigan, Ann Arbor, made the first systematic collection during the 1920s and 1930s. The crews of the Work Projects Administration (WPA) at the University of Texas, Austin, undertook the second phase of vertebrate collection from 1939 to 1941. One of the areas extensively quarried by the WPA crews was the Otis Chalk area in Howard County, under the direction of Grayson Meade.

After the Second World War, there was not much activity in the exploration of Dockum vertebrates. However, the work resumed in the early 1980s, when I began systematic exploration of the Dockum vertebrates with my students and collected a large number of spectacular specimens under the auspices of the National Geographic Society. We have opened three quarries and conducted extensive excavations: the Post and Boren quarries in Garza County and the Kirkpatrick quarry in Crosby County (fig. 5.2). The new collection that is housed at the Museum of Texas Tech University has come into prominence as one of the richest known Triassic vertebrate assemblages in the world.

The Post Quarry

In the 1980s, we had been working in the Post quarry in Garza County of West Texas for the past three summers, unearthing an array of spectacular new tetrapods from a 30-centimeter-thick, fine-grained mudstone unit of the Tecovas Formation of the Dockum Group. At the beginning of the summer of 1983, we were planning a large-scale excavation at the Post quarry. The bone-bearing deposits at this site consist primarily of massive jointed red mudstone with a blocky, columnar, or prismatic structure and poor stratification, representing a typical overbank flood-plain sequence. The quarry has produced a prolific array of new tetrapods in a single dense layer, including two small temnopondyl tetrapods, *Apachesaurus* and *Rileymillerus*; an unnamed dicynodont; a tritheledontid cynodont, *Pachygenelus*; two bipedal rauisuchians, *Postosuchus* and *Shuvosaurus*; a phytosaur, *Leptosuchus*; several aetosaur genera, such as *Typothorax*, *Paratypothorax,* and *Desmatosuchus*; a silesaurid, *Technosaurus*; a coelophysoid dinosaur; a primitive bird, *Protoavis*; and several groups of new and small dinosauromorphs still to be described (Chatterjee 1983, 1984, 1985, 1986, 1993; Lehman and Chatterjee 2005). Initially, a mass mortality event resulting

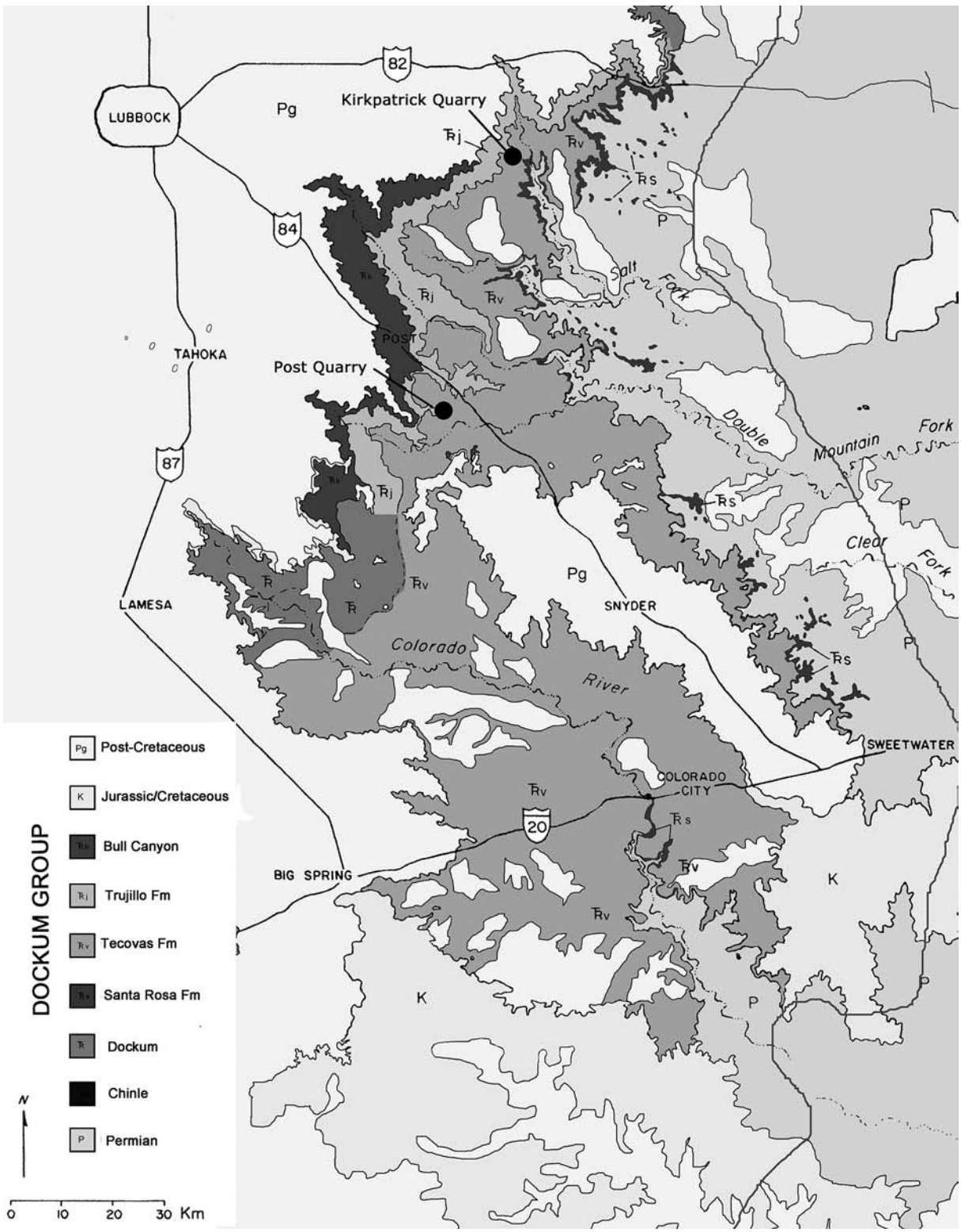


Figure 5.2. Generalized geological map of West Texas showing the exposures of Late Triassic continental sediments of the Dockum Group in the upper Brazos and Colorado River valleys. *Protoavis* bones have been recovered from the Kirkpatrick quarry and Post quarry, both from the Tecovas Formation of Carnian age.

from overbank flooding was suggested to explain the concentration of carcasses in the Post quarry (Chatterjee 1985). However, the usual disarticulated but associated condition of many skeletons and vague or marked current alignment of bone long axes suggests that some other long-term process of bone concentration was responsible for the initial accumulation and later dispersion of carcasses (Lehman and Chatterjee 2005). The vertebrate remains are variably preserved as articulated skeletons, partly articulated segments of skeletons, or associated but disarticulated skeletons of primarily terrestrial animals. Such sites often preserve small and delicate skeletal elements that together do not constitute an assemblage of hydraulically equivalent objects. Hence, neither concentration nor winnowing of carcasses by current action seems a likely mechanism for the resulting assemblages. Such sites sample primarily terrestrial habitats, and yield a diverse assemblage of trilophosaurs, therapsids, aetosaurs, rauisuchians, and dinosaurs that differ from the typical aquatic metoposaur-phytosaur dominated assemblages found in channel-related or lacustrine facies. Life and death of the terrestrial community in the overbank of a Triassic river were preserved nicely in the Post quarry. These fossils would become important components of the Late Triassic vertebrates in the American Southwest and would bring paleontologists from all over the world for comparative study and biostratigraphic correlation.

The Discovery of *Protoavis*

Little did I realize that the "Pandora's box" I was about to open when I picked up two partial skeletons of a tiny dinosaur out of the Post quarry mudstone during excavation in the summer of 1983 would create so much controversy and excitement. The finds of the two delicate skeletons from this multispecies bone bed were serendipitous. The fossils were exposed accidentally in a small mudstone block while removing the overburden with a heavy jackhammer (fig. 5.3). Some tiny bone fragments in a mudstone block caught my attention while we were clearing up the overburden to expose the bone bed. Once I looked at the dislodged block more closely, I saw an ensemble of disarticulated bones closely packed, including a string of vertebrae and hindlimb elements. Most intriguing was a tiny fused anklebone with a characteristic mesotarsal joint that looked like a theropod ankle. Because most of the skeletons were concealed in the matrix, we did not appreciate the importance of this discovery at the time. In my field notebook on June 17, 1983, I recorded this discovery:

> We found a juvenile skeleton of *Coelophysis* in a mudstone block that fits into my palm. The block broke into 2 pieces exposing more bones. The vertebrae are exceedingly small, less than a centimeter in length, yet the neural arches are fused to the centra. The astragalus-calcaneum looks like that of a theropod, but are fused to each other. The fusion of bones in this baby individual is unusual. No skull bones are visible. The specimen needs careful preparation.

Initially, I classified these specimens as a juvenile *Coelophysis* because these early theropods were common in the American Southwest (Chatterjee 1986). Hundreds of intact skeletons of *Coelophysis* have been reported from the coeval Chinle beds of the Whitaker quarry of Ghost Ranch in New Mexico, ranging in body length from 0.8 to 3 meters, and their presence in Texas is expected. In 1985, while I was studying a little theropod, *Alwalkeria*, from the Triassic of India (Chatterjee 1987b), I retrieved the Dockum specimens for comparison. The Dockum theropods were tiny animals compared to *Alwalkeria*; the bones were delicate, were jumbled together, and required careful preparation under a binocular microscope. It took almost six months to remove the matrix and prepare the material. Soon I began to realize that the Texas specimens represented two individuals of an unknown species never found before. They were not *Coelophysis*, nor did they resemble any known theropods. The most striking feature in the skull is the bird-like quadrate with an orbital process, where the quadrate head fits nicely into a socket of the squamosal. The squamosal is also reduced in avialan fashion, with the development of a zygomatic process. It lacks the descending process in front of the quadrate, indicating streptostyly of the quadrate, a typical avian hallmark. The jugal and quadratojugal form a horizontal bar. None of these features is known in any

A B

Figure 5.3. A, Post quarry in Garza County, Texas, where *Protoavis* skeletons were first found. B, jackhammer operation during the discovery of *Protoavis* in the summer of 1983. Two delicate skeletons of *Protoavis* were exposed accidentally near the blade of the jackhammer while graduate students were removing the overburden; *left*, Bryan J. Small; *right*, J. Bruce Moring.

nonavialan theropod. The temporal region is modified in avian fashion. The braincase is highly enlarged, with numerous pneumatic sinuses. Several postcranial characters, such as the strut-like coracoid, the furcula with a large hypocleidium, the heterocoelous cervicals, and the fused ilioischiadic plate, are present only in birds, not in any nonavian theropods.

Later, I collected a total of thirty-one isolated postcranial elements of *Protoavis* from the coeval lacustrine facies association of Tecovas Formation in the Kirkpatrick quarry in Crosby County, along with other microvertebrates. The preservation of bone is excellent in this quarry. The lacustrine beds contain a variety of burrows, coprolites, freshwater ostracods, fish, metoposaurs, and phytosaurs. Most likely, these lakes were formed by localized syndepositional subsistence of the flood-plain surfaces, induced by dissolution of Permian evaporite deposits that underlie the Dockum Group (Lehman and Chatterjee 2005). Here the fossils are concentrated in a thin layer of carbonate granule conglomerate intercalated with the red mudstone of the Tecovas Formation. Initially, I thought that the Post quarry represented the younger Bull Canyon Formation, but the Kirkpatrick quarry lies in the older Tecovas Formation. Recent detailed mapping and biostratigraphic correlation undertaken by my students, Jeff Martz and Bill Mueller, suggest that *Protoavis* fossils from both the Post quarry and the Kirkpatrick quarry occur entirely within the Tecovas Formation; many taxa between the Post quarry and the Kirkpatrick quarry are identical, indicating that these animals lived in the same time and that the beds between the two quarries are mappable and continuous.

After preparation and comparisons of the little theropod animal from the Post and Kirkpatrick quarries, I was excited and perplexed. Was it a bird or a theropod? For a long time, I debated and hesitated to commit myself. Anatomical details of this intriguing animal convinced me that it is more closely related to living birds than is *Archaeopteryx*. Moreover, the animal could fly, which is revealed by its flight apparatus. Many experts on fossil

birds such as Nick Hotton of Smithsonian Institution, Larry Martin and Larry Witmer of University of Kansas, Walter Bock of Columbia University, and Evgeny Kurochkin of the Russian Academy of Sciences examined the specimens and confirmed my identification that the newly found material exhibited a suite of distinct avialan traits. Even Stephen Jay Gould from Harvard University came to our museum to see the new Dockum bird and briefly mentioned the trip in his popular book, *Dinosaur in a Haystack*. It became clear to me that if *Archaeopteryx* is a bird, we must incorporate the Texas specimens as a more derived member of the avialan clade than *Archaeopteryx*. In 1986, National Geographic Society recruited John Ostrom, famous for his revolutionary theropod-bird hypothesis, to examine the Triassic fossils. Ostrom came to our museum, studied them, and reported to the society about his tentative identification of the specimens. Upon hearing his lukewarm approval of avialan identity, the National Geographic Society announced the discovery of the earliest Texas bird fossils in a press release that got national and international media coverage and ignited the storm of controversy that still persists to this day.

I presented my study on the Triassic bird fossils in various national and international meetings to get feedback from the audiences (Chatterjee 1987a, 1994). After many years of research and reflection, I finally named these animals *Protoavis texensis* and described the cranial anatomy in the *Philosophical Transactions of the Royal Society of London*, in a sixty-five-page monograph in 1991 along with larger issues such as the evolution of cranial kinesis, brain development, and the systematics of Mesozoic birds; later my findings on the postcranial material of *Protoavis* and phylogenetic analysis of Mesozoic birds were published in a one hundred-page *Palaeontographica* monograph in 1999, addressing the evolution of locomotor modules in birds. In both publications, all bird bones collected from the Dockum Group from both quarries were accommodated into one species, *Protoavis texensis*. The bones are now housed at the Museum of Texas Tech University. I supported the orthodox view of the theropod relationships of birds (Ostrom 1976a; Gauthier 1986), and concluded that *Protoavis* is closer to modern birds than *Archaeopteryx*. I found nearly every skeletal element is represented among these specimens, though some critical bones were damaged and open to other interpretations (Chatterjee 1995). A popular account of *Protoavis* was also included in the first edition of this book, which also covered a wide variety of topics, including the origin and early radiation of birds, the evolution of flight, and the biotic crisis at the end-Cretaceous extinction when birds nearly died but rebounded with vigor in the early Tertiary period (Chatterjee 1997).

A Portrait of *Protoavis*

Before we start to look at different kinds of Mesozoic birds and to appreciate the origin and diversity of this group, we need to look more closely at the anatomy of *Protoavis*. Being the earliest bird, its skeleton provides a general body plan that has been modified to meet the rigorous demands of flight. The skeleton of *Protoavis* has a basic avialan structure as seen in *Jeholornis* but retains several primitive characteristics of nonavialan theropods—an example of mosaic evolution.

Protoavis was extremely small relative to nonavialan dinosaurs. The large individual of *Protoavis* (holotype, TTU P 9200) is a pheasant-sized bird with a long bony tail. Its total length is about 60 centimeters, corresponding in size to the Solnhofen specimen of *Archaeopteryx*. The smaller individual (paratype, TTU P 9201) probably represents a juvenile individual, but like modern birds, the neural arch and centrum are fused in this early stage. It is about half the size of the holotype and matches the size of the Eichstätt specimen of *Archaeopteryx*.

The Skull

As in most Mesozoic birds, the cranial bones are not fused in *Protoavis*. They are thin and delicate, and they tend to become somewhat disarticulated during fossilization. The skull is relatively small: 74 millimeters long, 38 millimeters wide, and 32 millimeters deep as restored in the holotype (fig. 5.4). The short snout, enormous orbits, and inflated braincase have crowded the cheek region. Many of the bars behind the orbits and between the two

temporal openings have disappeared. The skull shows several avian hallmarks in lateral aspect, including a modified diapsid condition, the postorbital process, the zygomatic process, and the orbital process that are lacking in *Archaeopteryx*. The teeth are retained at the tip of the jaws, but the posterior teeth have been lost. The edentulous region was evidently encased by horny sheath, as in modern birds. The three premaxillary teeth oppose the two dentary teeth; each tooth is small, is compressed sideways, and lacks serration. The naris is bounded by the premaxilla and the nasal. The maxilla is edentulous and has an ascending process in front of the antorbital fenestra that underlies the nasal. The prefrontal is absent, as in other birds. The frontal is an elegant, inflated bone that surrounds the orbit. The orbits are very large, about one-third of the skull length, and are forwardly placed, suggesting stereoscopic vision. The postorbital bone has been lost. In its place, the frontal and laterosphenoid form a postorbital process for the attachment of the postorbital ligament. Rostrally, the frontal becomes narrow and flat to form a flexible hinge with the nasal. Behind the frontal, the parietal is transversely arched and contacts the squamosal laterally. The lacrimal forms a vertical bar between the orbit and the antorbital opening and has a sliding joint with the jugal. The jugal and quadratojugal form a slender jugal bar without any vertical struts. The quadratojugal, in turn, develops a flexible pin joint with the quadrate. Because of the elimination of the diapsid arches and the squamosal-quadratojugal bar, the quadrate becomes streptostylic. The squamosal is considerably reduced; it shows a distinctive zygomatic process and the lack of a descending process in front of the quadrate. It has developed a separate ventral cotyle for the quadrate head to form the ball-and-socket joint.

In the palate, the choana has been shifted considerably backward so that the palatal components of the maxillae and the intervening vomers contribute to the secondary palate, as in primitive birds (fig. 5.4C). The vomers are long and fused rostrally to lie between the premaxillae. Caudally, they are separated and meet the pterygoids. The palatine is a long, slender bone that forms the lateral margin of the choana. The pterygoid is reduced considerably rostrally. It runs backward and outward to the ventral condyle of the quadrate, to which it is loosely attached. The ectopterygoid has been lost, as in birds, to make the palate more mobile. The quadrate has a single, spherical head but shows several avialan attributes: a free orbital process, a ventral condylar articulation with the pterygoid, a lateral cotylus for the quadratojugal, a tricondylar articulation with the mandible, and the acquisition of streptostyly.

The braincase (figs. 5.4D, 5.5A–B) is inflated and shows neurosensory specialization possibly associated with balance, coordination, muscular control, and flight. The occipital condyle is fairly small relative to the foramen magnum. A distinctive epiotic bone is present on the posterior aspect of the occiput and is separated from the supraoccipital by a sinus canal. Medially, a large and deep floccular recess occurs between the epiotic and prootic; this recess is surrounded by a bony tube for the rostral vertical semicircular canal (fig. 5.5B). The otic capsule is built in avian fashion and shows three foramina clustered together in the tympanic recess: the fenestra ovalis in the front, the fenestra pseudorotunda behind, and the caudal tympanic recess at the caudodorsal corner. Behind the fenestra pseudorotunda, a large metotic strut is added to the exoccipital so that the vagus foramen (X) has been diverted backward and emerges through a single foramen in the occiput. Lateral to it lies the exit for the hypoglossal (XII) nerve. A parabasal notch lateral to the vagus foramen affords passage for the internal carotid artery. This notch continues forward as a bony parabasal canal. The middle ear cavity region is highly pneumatized, and all of the air sinuses of birds—rostral, caudal, dorsal, quadrate, and articular tympanic recesses—are present. The functions of these tympanic recesses are not well understood but may be linked to better detection of low-frequency sound (Witmer 1990). As in living birds, the rostral tympanic recess in *Protoavis* shows contralateral communication that might provide critical directional information in three-dimensional space (Rosowki and Saunders 1980). The basioccipital-basisphenoid complex is extensively permeated by pneumatic cavities.

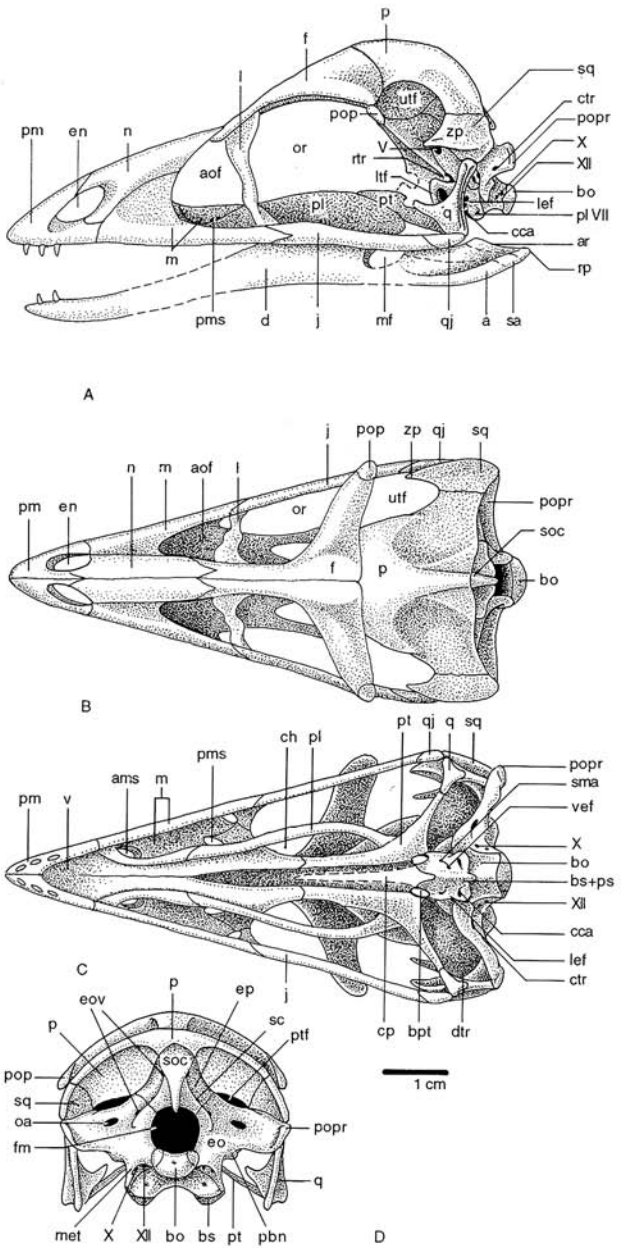


Figure 5.4. *Protoavis texensis*; composite restoration of the skull representing the size of the holotype, TTU P 9200. A, left lateral view; B, dorsal view; C, ventral view; D, occipital view (after Chatterjee 1997). Abbreviations: a, angular; ams, anterior maxillary sinus; aof, antorbital fenestra; ar, articular; bo, basioccipital; bpt, basipterygoid process; bs, basisphenoid; cca, foramen for cerebral carotid artery; ch, choana; cp, cultriform process; ctr, caudal tympanic recess; d, dentary; dtr, dorsal tympanic recess; en, external naris; eo, exoccipital; eov, foramen for external occipital vein; ep, epiotic; f, frontal; fm, foramen magnum; fo, fenestra ovalis; fpr, fenestra pseudorotunda; j, jugal; l, lacrimal; lef, lateral Eustachian foramen; ltf, lower temporal fenestra; m, maxilla; met, metotic strut; mf, mandibular foramen; n, nasal; oa, occipital artery foramen; opr, orbital process; or, orbit; p, parietal; pbn, parabasal notch; pl, palatine; pm, premaxilla; pms, posterior maxillary sinus; pop, postorbital process; popr, paroccipital process; pr, prootic; ps, parasphenoid; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; rp, retroarticular process; rtr, rostral tympanic recess; sa, surangular; sc, sinus canal; sma, foramen for sphenomaxillary artery; soc, supraoccipital; sq, squamosal; utf, upper temporal fenestra; v, vomer; vef, ventral Eustachian foramen; zp, zygomatic process; Roman numerals indicate the foramina for cranial nerves.

The bony Eustachian tube is enclosed within the parasphenoid; its lateral opening is highly enlarged, whereas its ventral opening lies medial to the basipterygoid process.

The lower jaw (fig. 5.4A) is slender, tapers slightly forward, and is very shallow for most of its length. The mandibular symphysis is ossified, and the postdentary bones are fused. The external mandibular foramen is small and elongated and is bordered by a rostral fossa. The surangular shows a lateral process for the attachment of the postorbital ligament. The retroarticular process, formed mostly by a posterior extension of the articular bone, is well developed.

The Vertebral Column

It is estimated that there are twelve cervical, nine dorsal, six sacral, and twenty caudal vertebrae in *Protoavis*. The

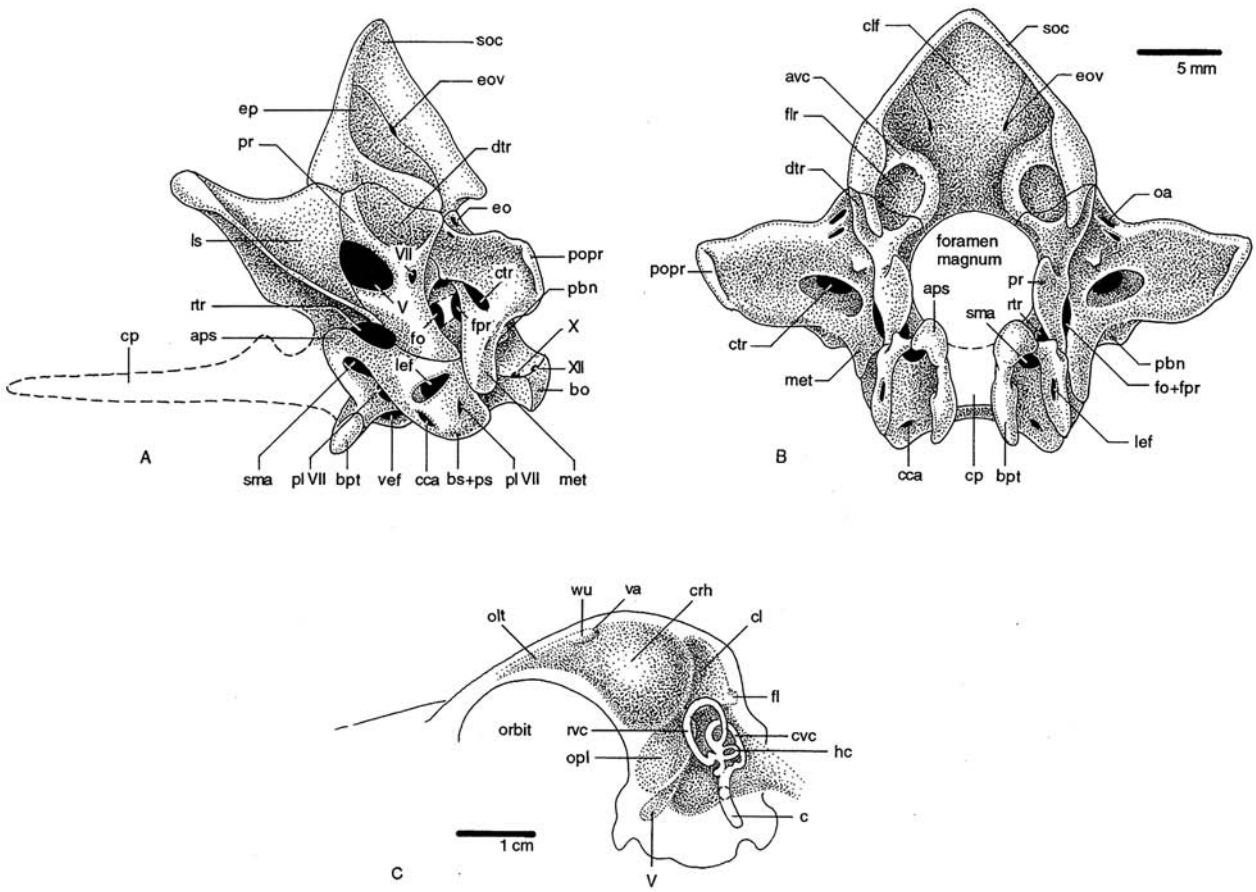


Figure 5.5. *Protoavis texensis*; composite restoration of the braincase and endocast, representing the size of the holotype (after Chatterjee 1997). A, left lateral view; B, cranial view; C, restoration of the brain from the endocast, lateral view (Chatterjee 1997). Abbreviations: aps, alaparasphenoid; bo, basioccipital; bpt, basipterygoid process; c, cochlear duct; cca, foramen for cerebral carotid artery; cl, cerebellum; clf, cerebellar fossa; cp, cultriform process; crh, cerebral hemisphere; ctr, caudal tympanic recess; cvc, caudal vertical canal; dtr, dorsal tympanic recess; eoa, foramen for external occipital vein; ep, epiotic; euf, foramen for Eustachian canal; fl, floccular lobe; flr, floccular recess; fm, foramen magnum; fpr, fenestra pseudorotunda; hc, horizontal canal; ic, foramen for internal carotid artery; lef, lateral Eustachian canal; ls, laterosphenoid; met, metotic strut; oa, foramen for occipital artery; olt, olfactory tract; opl, optic lobe; pbn, parabasal notch; popr, paroccipital process; pr, prootic; rtr, rostral tympanic recess; rvc, rostral vertical canal; sma, foramen for sphenomaxillary artery; soc, supraoccipital; va, vallecula; vef, ventral Eustachian foramen; wu, wulst; Roman numerals indicate the foramina for cranial nerves.

heterocoelous centra and hypapophyses in the anterior cervical region of *Protoavis* (fig. 5.6A) are highly derived features among Mesozoic birds. These features are restricted to few Cretaceous taxa, such as Enantiornithes, Hesperornithiformes, *Patagopteryx*, and the Antarctic loon *Polarornis*. Each prezygapophysis in this region faces forward and forms a convex rolling surface in lateral aspect. The curvature of the prezygapophyseal facet approximates a circular arc, permitting a continuous range of movement of the neck without obvious osteological stops. The long and flexible neck with the development of heterocoelous vertebrae permitted *Protoavis* a wide range of movement of the head, which functioned as a universal tool. The neural spines are atrophied. The vertebral column is incompletely preserved. The cervical vertebrae are elongate, while the centrum is amphicoelous (with both the anterior and the posterior surfaces being concave) to platycoelous (flat or concave ventrally

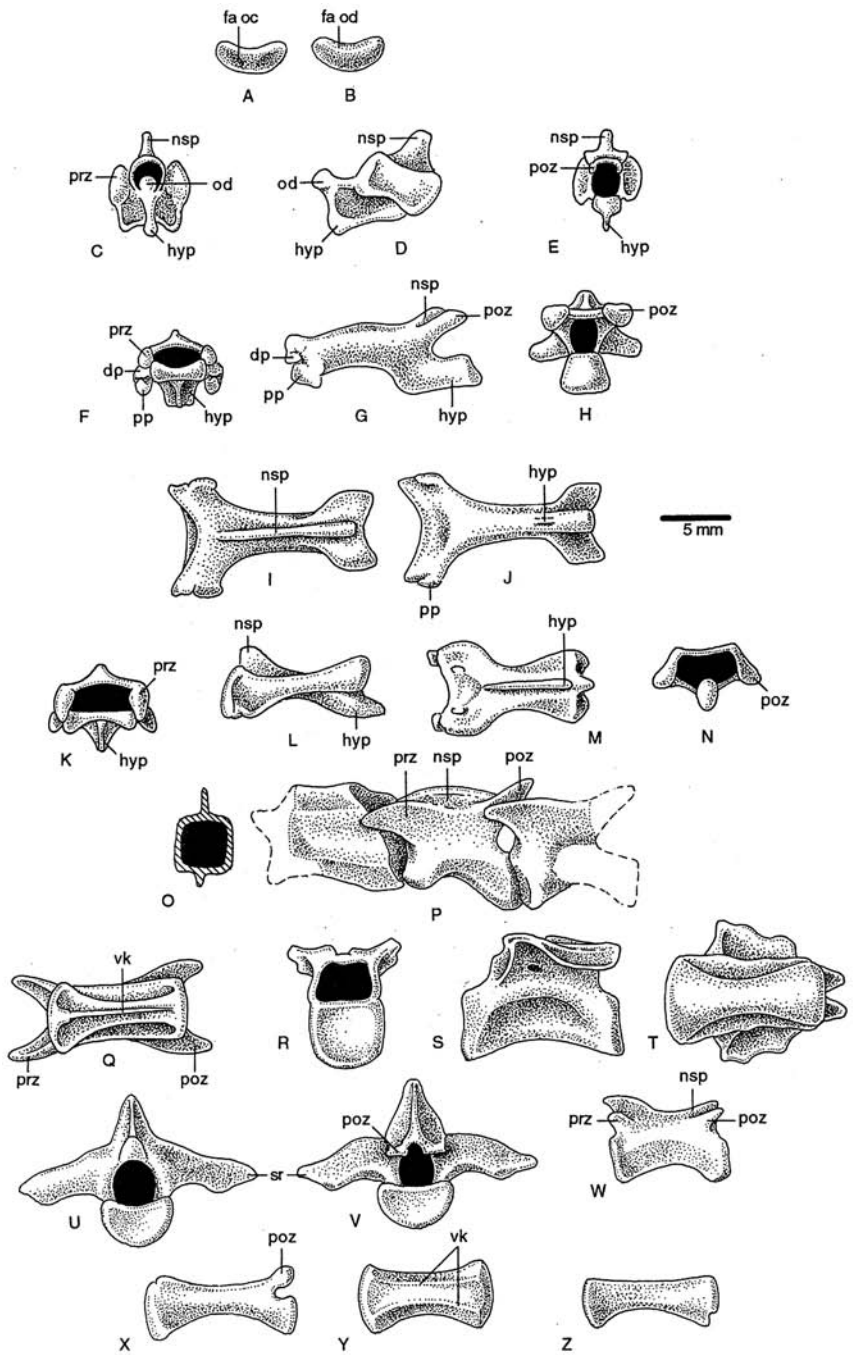


Figure 5.6. *Protoavis texensis*, vertebral column, representing the size of the paratype TTU P 9201 (after Chatterjee 1997). A and B, cranial and caudal views of the atlas intercentrum. C–E, cranial, lateral, and caudal views of the axis. F–J, cranial, lateral, caudal, dorsal, and ventral views of the third cervical; note the heterocoelous centrum and hypapophysis. K–N, cranial, lateral, caudal, and ventral views of the fourth cervical. O, cross section of the ninth cervical showing the hollow core. P, lateral view of the ninth, tenth, and eleventh cervicals. Q, ventral view of the tenth cervical. R–T, rostral, lateral, and ventral views of the first dorsal. U and V, rostral and caudal views of the first sacral. W, lateral view of the fourth caudal. X, lateral view of the thirteenth caudal. Y, ventral view of the sixth caudal. Z, lateral view of the twentieth caudal (after Chatterjee 1997). Abbreviations: dp, diapophysis; fa ac, facet for occipital condyle; fa od, facet for odontoid; hyp, hypapophysis; nsp, neural spine; od, odontoid; pp, parapophysis; poz, postzygapophysis; prz, prezygapophysis; sr, sacral rib; vk, ventral keel.

and convex dorsally); it has a large hollow core in cross section with a paper-thin bony shell around it in camellate fashion. The absence of a pleurocoel on the centra may be attributed to the juvenile nature of the specimen (TTU P 9200), but lateral depressions on the centra and pneumatic chambers in the neural arch are present throughout the column. In several isolated specimens, pleurocoels are preserved. The neural canal is highly enlarged relative to the centrum, presumably indicating a higher demand for nerve signal traffic. The trunk appears to be short, horizontal, and rigid without any sign of fusion. The sacrum is poorly preserved; the first sacral shows the characteristic expanded ribs. *Protoavis* had a long bony tail similar to that of *Archaeopteryx*, without any development of a pygostyle at the end. The caudal centra are weakly amphicoelous and maintain a uniform length throughout the column but decrease in diameter posteriorly. The terminal tail vertebrae become highly slender and delicate rods. They lack both zygapophyses and intersegmental mobility; they probably functioned together as a stiff unit to control pitch during flight.

The Shoulder Girdle

The shoulder girdle of *Protoavis* was designed on the same mechanical principle as that of modern birds, with the development of a strut-like coracoid, a triosseal canal for the supracoracoideus pulley, a spring-like furcula bearing a hypocleidium, and a keeled sternum (fig. 5.7A–B). The scapula is a long and tapering bone that meets the coracoid in a flexible manner. A pneumatopore is present near the acromion, where the scapula joins the furcula. The glenoid cavity faces outward and upward, which permits dorsoventral movement of the humerus. The coracoid is long and stout and bears both procoracoid and acrocoracoid processes. The sternum has a ventral keel for the attachment of two sets of flight muscles, the pectoralis and supracoracoideus (fig. 5.7M). Dorsally, the sternal basin is hollow and is pierced by several pneumatic foramina. The furcula is very similar to that of a chicken (*Gallus*) in morphology, with a large hypocleidium. It would act as a spring between two shoulder girdles, facilitating inflation and deflation of the clavicular sac during flight (Jenkins et al. 1988).

The Wing

Like living birds, *Protoavis* acquired two independent and specialized methods of locomotion, flying with the forelimbs and walking with the hindlimbs. *Protoavis* was an obligatory biped, as indicated by the development of the swivel wrist joint, which would restrict hand movement for terrestrial locomotion. The forelimb developed a linkage system at the elbow and wrist joints and was modified into a collapsible wing. The humerus (fig. 5.7C–H) of *Protoavis* is remarkably avialan. It is a strong, tubular bone; the two expanded ends lie in the same plane. Proximally, there is a pronounced head that fits into the glenoid. In cranial aspect, a ligamental depression occurs just below the head for the attachment of the supracoracoideus muscle. Farther dorsally the deltopectoral crest is expanded and has a ridge-like projection for the insertion of the pectoralis muscle. At the ventral side, the bicipital crest, an unusually advanced feature in a Triassic bird, is weakly developed. Both dorsal and ventral tuberosities are encountered near the proximal end, but they are relatively subdued in comparison to those in modern birds. A shallow pneumatic fossa occurs below the ventral tuberosity but is not pneumatized by the foramen. Here the head is separated from the ventral tuberosity by a capital groove. The shaft is long, hollow, and flattened cranially. The distal expansions show two well-defined, asymmetrical condyles for the radius and the ulna, respectively. The dorsal, or radial, condyle is larger and more pronounced, elongated parallel to the axis of the bone. The ventral or ulnar condyle is almost spherical and continues onto the posterior surface, where it is bordered by a deep olecranon fossa. Both ectepicondyles and entepicondyles are well developed on the dorsal and ventral borders of the distal end.

The radius is a straight cylindrical bone that is slimmer than the ulna. Proximally, it shows a concavity for the reception of the humerus; distally, it is expanded to receive the radiale. The ulna is a curved bone with an olecranon process at the proximal end. The shaft is damaged and bears a series of faint bumps similar to quill knobs (fig. 5.7I), but their identity is uncertain. The distal end is slightly expanded into a trochlear surface and

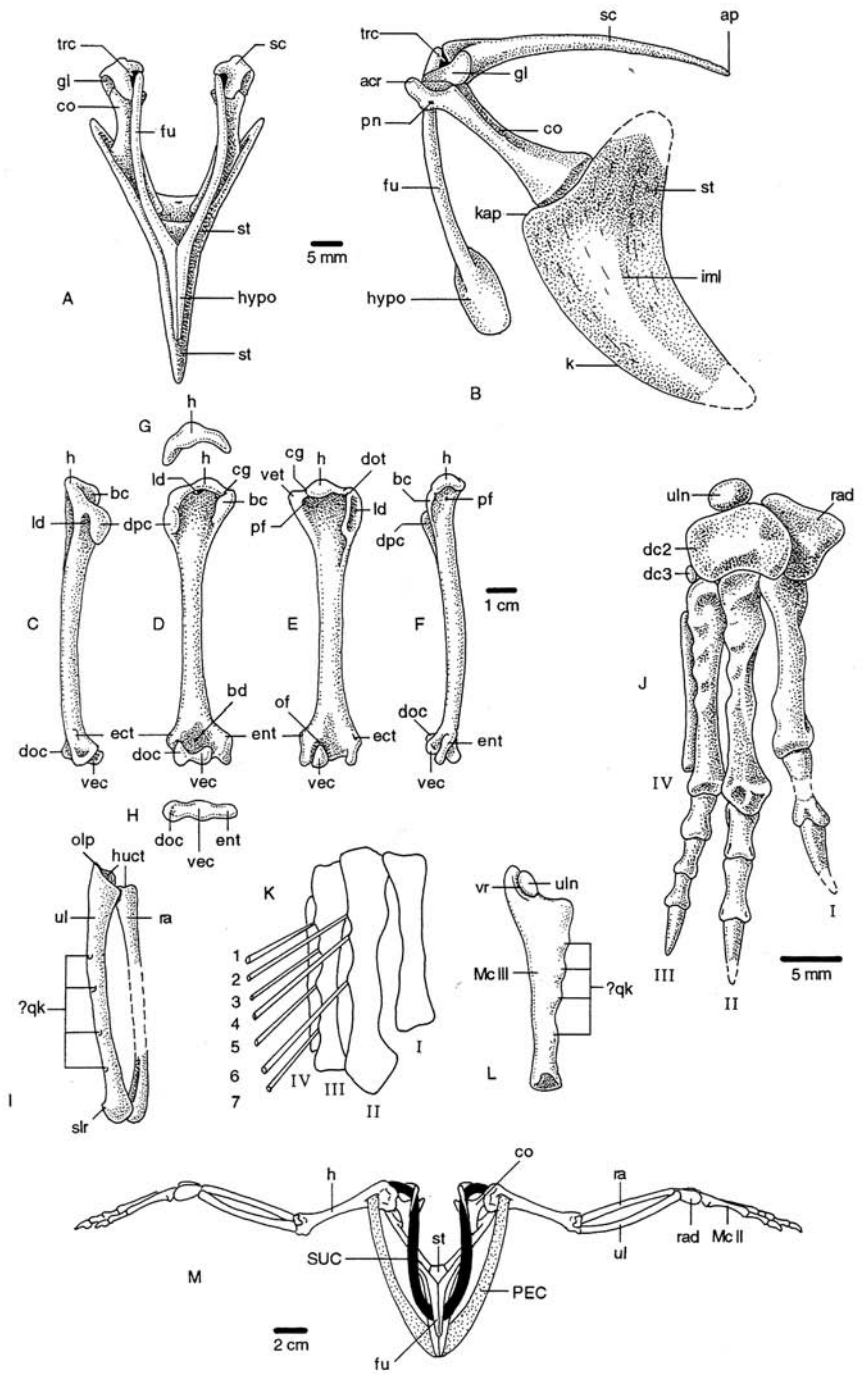


Figure 5.7. *Protoavis texensis*, composite restoration of the shoulder girdle and forelimb, representing the size of the holotype (after Chatterjee 1997). A and B, cranial and lateral views of the shoulder girdle. C–H, dorsal, cranial, caudal, ventral, proximal, and distal views of the right humerus. I, dorsal view of the right radius and ulna. J, dorsal view of the right manus. K, outlines of metacarpals showing the quill knobs for attachment of primaries. L, caudal view of metacarpal III showing its interlocking articulation with the ulnare by the ventral ridge. M, shoulder girdle and extended wings in cranial view to show the action of the flight muscles. (Chatterjee 1995.) Abbreviations: acr, acrocoracoid; ap, apex; bc, bicipital crest; bd, brachial depression; bt, biceps tubercle; cg, capital groove; co, coracoid; dc, distal carpal; doc, dorsal condyle; dot, dorsal tuberosity; dpc, deltopectoral crest; ect, ectepicondyle; ent, entepicondyle; fu, furcula; gl, glenoid fossa; h, head; hu, humerus; huct, humeral cotyle; hypo, hypocleidium; iml, intermuscular lamina; k, keel; kap, keel apex; ld, ligamental depression; mc, metacarpal; of, olecranon fossa; olp, olecranon process; PEC, pectoralis muscle; pf, pneumatic fossa; pn, pneumatic foramen; qk, quill knobs; ra, radius; rad, radiale; sc, scapula; str, semilunate ridge; st, sternum; stb, sternal basin; SUC, supracoracoideus muscle; trc, triosseal canal; ul, ulna; uln, ulnare; vec, central condyle; vr, ventral ridge; Roman numerals indicate the digits in the manus.

shows a weak semilunate ridge on the dorsal edge for articulation with the ulnare.

The manus is beautifully preserved in *Protoavis*. It shows four separate carpal and four metacarpal bones without any sign of fusion (fig. 5.7J). Four metacarpals are also present in embryonic birds, but in adults the first three metacarpals are fused with the distal two carpal bones to form the carpometacarpus, whereas the fourth metacarpal disappears.

The wrist is intact in *Protoavis*. The radiale is ovoid in outline and considerably larger than the ulnare. Proximally, it has a distinct facet for the radius; distally, it has a rolling surface for distal carpal 2. The ulnare is a small disc, lying between the ulna and distal carpal 2. The smallest carpal bone, proximate to metacarpal III, is identified as distal carpal 3. Distal carpal 2 is the largest carpal element and has a well-designed joint surface. Proximally, it has a pulley-like groove, the carpal trochlea, which extends along the whole width to form the swivel joint. This allows the hand to move along the plane of the wing surface. Unlike the condition of maniraptoran theropods, distally, the semilunate bone has a single socket for reception of metacarpal II. A similar distal carpal is known in *Confuciusornis*. The hand has three functional digits, with a vestige of metacarpal IV. Metacarpal I shows a subdued extensor process. Metacarpal II is the most robust and longest bone in the series. Metacarpal III has a ventral ridge at the proximal end to interlock with the ulnare. Both metacarpals II and III appear to fuse at the ends to form a large intermetacarpal space. They bear a series of quill knobs for the attachment of primary feathers. There are about seven quill knobs, arranged alternately on the dorsal surfaces of metacarpals II and III. Unlike modern birds, *Protoavis* shows that both metacarpals might have supported primary feathers in alternate fashion, while metacarpal IV provided lateral support for the shaft of the feathers. Metacarpals I–III retain phalanges and terminal claws, with the formula being 2-3-4-0-x.

The Pelvic Girdle

The pelvis of *Protoavis* shows derived features not reported in many Mesozoic birds: (1) the ischium is rotated parallel to the ilium and fused distally to enclose the ilioischiadic foramen; (2) the ischium and pubis are open ventrally without any symphysis; (3) there is a renal fossa; (4) the ischiadic peduncle of the ilium is short and reduced; and (5) the pubis is relatively short, without any sign of distal expansion, or "foot."

The ilium expands into a broad, flaring blade with long preacetabular and postacetabular processes as seen in some oviraptorosaurs; the former is hooked and bears a prominent ventral projection for the attachment of the femoral protractor muscle (fig. 5.8A–C). The opisthopubic pelvis and the cranial elongation of the preacetabular process may be linked to the subhorizontal attitude of the femur. The acetabulum is very shallow, circular, and completely perforated to receive the inturned head of the femur. The medial surface of the ilium is very complex and shows the renal fossa on the postacetabular area to accommodate the kidney. The fossa is bordered medially by the ilioischiadic pila, as in some modern birds, to reinforce the ilioischiadic plate. The renal fossa is a diagnostic feature of birds.

The ischium is a narrow, bony plate directed backward to fuse with the ilium; the line of fusion is visible on the lateral aspect, but the fusion is obscured medially by the ilioischiadic pila. Proximally, the bone is forked cranially around the acetabulum; the pubic process is a narrow rod, whereas the ischiadic process is broad and stout, bearing a weak antitrochanter process. Immediately below the pubic process is a prominent obturator process on the ischium.

The pubis, approximately equal to the ilium in length, is considerably longer and slimmer than the ischium. It projects downward and backward at a 45° angle to the horizontal and is separated from the ischiadic shaft by a triangular gap. In modern birds, the pubis lies alongside the ischium and contacts the obturator process to enclose the obturator foramen. The proximal end of the pubis is expanded and differentiates into a large iliac and a narrow ischiadic process around the acetabulum. A pectineal process on the pubis near the acetabulum is the origin of the ambiens muscle. The shaft is long and narrow without any distal expansion or symphysis, unlike the condition in *Archaeopteryx*.

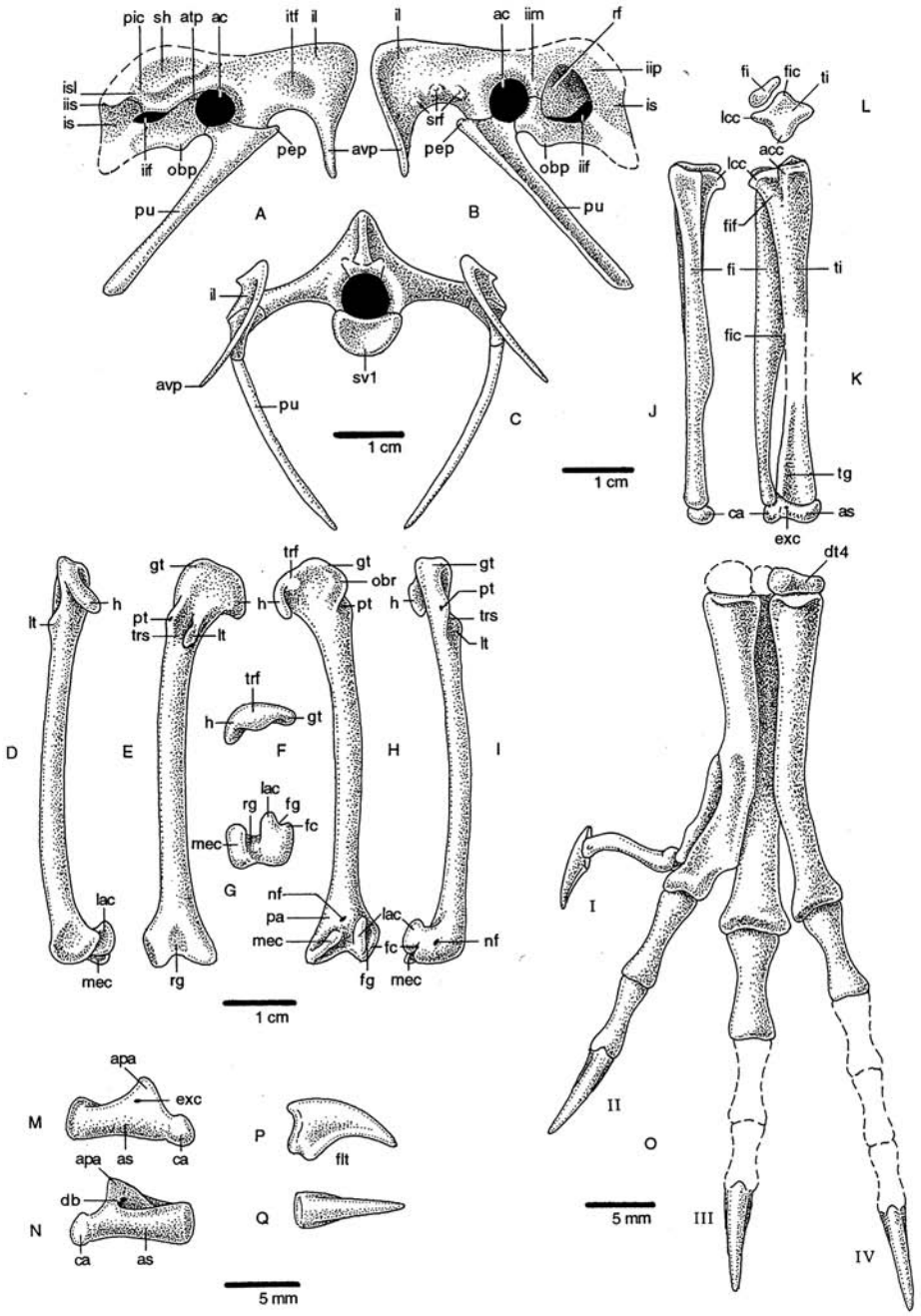


Figure 5.8. *Protoavis texensis*, composite restoration of the pelvic girdle and hindlimb, representing the size of the holotype (after Chatterjee 1997). A–C, lateral, medial, and cranial views of the right pelvic girdle. D–I, medial, cranial, proximal, distal, caudal, and lateral views of the right femur. J–L, lateral, caudal, and proximal views of the right tibia and fibula. M–N, cranial and caudal views of the left astragalocalcaneum. O, anterior view of the left pes. P–Q, lateral and dorsal views of a claw of the third digit. Abbreviations: acc, anterior cnemial crest; ac, acetabulum; apa, ascending process of the astragalus; avp, anteroventral process of the ilium; ca, calcaneum; db, dorsal basin; dt, distal tarsal; exc, extensor canal; fc, fibular condyle; fg, fibular groove; fi, fibula; fic, fibular crest; flt, flexor tubercle; gt, greater trochanter; h, head; iif, ilioischiadic foramen; iim, intermedial iliac crest; iip, ilioischiadic pila; iis, ilioischiadic suture; il, ilium; ilp, iliac process; is, ischium; isl, ischiadic lamina; isp, ischiadic process; itf, iliotrochanteric fossa; lac, lateral condyle; lcc, lateral cnemial crest; lt, lesser trochanter; mec, medial condyle; mt, metatarsal; nf, nutrient foramen; obp, obturator process; obr, obturator ridge; pa, popliteal area; pep, pectineal process; pic, posterior iliac crest; pt, posterior trochanter; pu, pubis; rf, renal fossa; rg, rotular groove; srf, sacral rib facets; sv1, first sacral vertebra; ti, tibia; tic, tibial crest; tg, tendinal groove; tro, trochlea; trs, trochanteric shelf; Roman numerals indicate the digits in the pes.

The Hindlimb

The hindlimbs of *Protoavis*, as in many Mesozoic birds, are intermediate in morphology between those of nonavialan theropods and those of modern birds. The femur is a cylindrical bone with a slight craniocaudal curvature. The head is oval in outline and broadly convex to fit into the acetabulum. The greater trochanter is weakly developed and contacts the antitrochanter on the acetabulum. From the greater trochanter a prominent obturator ridge curves distally as an oblique rugose crest on the caudal aspect of the shaft. The posterior trochanter, a muscle scar recognized in dromaeosaurs and *Archaeopteryx* by Ostrom (1976a), is also present in *Protoavis*. It occurs immediately below the greater trochanter. Unlike modern birds, *Protoavis* shows the primitive presence of the lesser trochanter. It projects as a conical boss below the head on the cranial surface and is set off from the shaft by a prominent shelf. The shaft is hollow, thin-walled, and oval in cross section. Distally, the femur flares into medial and lateral condyles for articulation with the tibia. The lateral condyle is highly pronounced and is separated from the fibular condyle by the fibular groove. The distal end is pierced by two nutrient foramina, one at the popliteal space and the other at the site of flexor attachment. I have observed these foramina in several species of modern birds.

The proximal head of the tibia is characteristically avialan, with the development of both lateral and cranial cnemial crests (fig. 5.8J–K). The cranial cnemial crest is an avialan feature that is absent in *Archaeopteryx*. A well-defined fibular crest to which the fibula is attached lies behind the lateral cnemial crest. The distal end is slightly inflated and is notched for the ascending process of the astragalus. Unlike modern birds, *Protoavis* has a tibia that is not fused with the proximal tarsal bones to form the tibiotarsus.

The fibula is a narrow, slender rod approximately equal in length to the tibia; it does not show any sign of fusion or reduction. A similar primitive fibula is known in several Mesozoic birds (e.g., *Archaeopteryx* and *Sinornis*). The proximal end is spatulate and is closely appressed to the fibular crest of the tibia. The shaft has an unusual tibial crest along the medial margin; this crest wraps tightly around the tibia. The distal end is oval and fits nicely into a corresponding socket of the calcaneum.

The pes is anisodactyl; the hallux is large, opposable, and fully reversed (fig. 5.8O). Metatarsal I is reduced to a splint and articulates with the distal end of metatarsal II. The long opposable hallux situated on the lower side of metatarsal II clearly indicates the development of a grasping foot. The central metatarsals (II–IV) are stout, elongated, and tightly appressed proximally in such a fashion that metatarsal III is proximally overlapped by metatarsal II and metatarsal IV in the cranial aspect. The distal trochlear surface of metatarsal III is symmetrical, while those of metatarsals II and IV are oblique and divergent. Metatarsal V is absent. The first four digits terminate in large, compressed, recurved claws with well-developed flexor tubercles, which are indicative of climbing or perching (fig. 5.8P–Q). *Protoavis* apparently possessed the capacity for tree climbing as well as bipedal walking.

The Brain and Sense Organs

Although soft parts are not preserved in the fossil vertebrates, the braincase contains various internal molds that can reveal a great deal of information about the morphology of the neurosensory organs it housed. The fossil record may provide important clues to the evolutionary pattern of brain, behavior, intelligence, and senses of extinct vertebrates.

The vertebrate brain is an extremely complex organ whose different components have been fashioned by 500 million years of natural selection. Simply making an internal cast of the cranial cavity one can see the architecture of the brain. This internal cast, or endocast, reveals the external morphology and size of the brain, especially in birds and mammals, thus providing crucial information about behavior and intelligence. In rare cases, natural endocasts are preserved in the fossils. Endocasts have been made for some theropods in a phylogenetic context to discover when and why brain enlargement might have taken place. In the theropod lineage, as I explain later, the enlargement of the brain may be critically linked to arboreal adaptation that demanded three-dimensional

orientation in space. The relatively large brains in both birds and primates in comparison to those of their terrestrial counterparts might be linked to arboreal adaptation in a three-dimensional world. Arboreal lifestyle demands not only neurosensory specializations but also highly refined balance and stability. The prime movers in avialan encephalization appear to be the arboreal adaptation of small theropods.

Brain Morphology

Information on the architecture of brains of extinct vertebrates has come from three sources: naturally occurring endocasts, latex endocasts of the brain cavity, and x-ray computed tomography of the braincase (i.e., virtual endocasts). I have used latex endocasts to study the brain morphology of *Protoavis*. Its brain, like that of modern birds, seems to have filled the cranial cavity almost completely; thus, the endocast provides a broad picture of the size and shape of the brain. The brain is differentiated into three segments from front to back in the avialan fashion: the cerebrum, optic lobes, and cerebellum. The brain is large and deep, oriented horizontally to form an arc around the back of the orbit (figs. 5.5C, 5.9A). At the front of the cerebrum, the olfactory lobes are short and reduced, reflecting poor development of the sense of smell. The cerebral hemispheres are expanded with the development of the visual wulst, bordered by a shallow vallecula laterally (fig. 5.9B). The wulst shows a small bulge on the dorsal surface. Cerebral enlargement indicates integration of the senses and enhanced intelligence in *Protoavis*. The enlargement of the cerebrum has led to its contact with the cerebellum dorsally, thus displacing the optic lobes ventrally and laterally. The large optic lobes must have played an important role in processing visual information. The cerebellum is largely associated with balance, muscular coordination, and posture, all so important to flying animals. In *Protoavis*, the cerebellum is fairly large and erect, with a dorsal swelling, and is housed between the parietal and the supraoccipital. A large and prominent floccular lobe extends from the lateral side of the cerebellum. This feature may be linked to bipedalism, for which balance is important. The flocculi are generally absent or minute in quadrupedal dinosaurs. The ventral swelling of the medulla into the pons indicates interconnection of the cerebrum with the cerebellum to mediate the complex motor activity of early birds. Below the cerebellum the medulla extends caudally and is the site of origin for the last eight (V–XII) cranial nerves. Only those cranial nerves responsible for smell and vision are located rostral to the medulla.

The gradual modification of brain morphology from primitive archosaurs to modern birds is shown in figure 5.9. Among archosaurs, the crocodiles (fig. 5.9F) and most nonavialan dinosaurs show a primitive pattern of brain morphology where the forebrain, midbrain, and hindbrain are narrow, elongate, and serially arranged. Brains of the nonavialan maniraptoran and pterosaur approach avialan morphology, with cerebral expansion and lateral displacement of the optic lobes (fig. 5.9E). This spatial rearrangement of the brain components may indicate similar neurosensory specialization associated with visual acuity, balance, and coordination in a three-dimensional world.

Encephalization and Intelligence

Brain size varies considerably among vertebrates, depending on their level of activity, mode of life, and intelligence. Like other organs, the brain is large or small in different animals according to whether body size is large or small. For example, the elephant brain is almost four times larger than the human brain. That does not mean that elephants are more intelligent than humans. Absolute brain size is not a reliable correlate of intelligence. What is needed is a method of estimating relative brain size in relation to body size.

For more than a century, it has been known that the relationship between brain weight and body weight is not linear but exponential; brain weight increases more slowly than body weight from a small to large animal within a single group. Edward Drinker Cope, a great nineteenth-century paleontologist, observed that, in an evolutionary lineage, the animals were steadily increasing in size. Most evolutionary brain enlargement is merely the result of the entire animal growing bigger. Encephalization, a measure

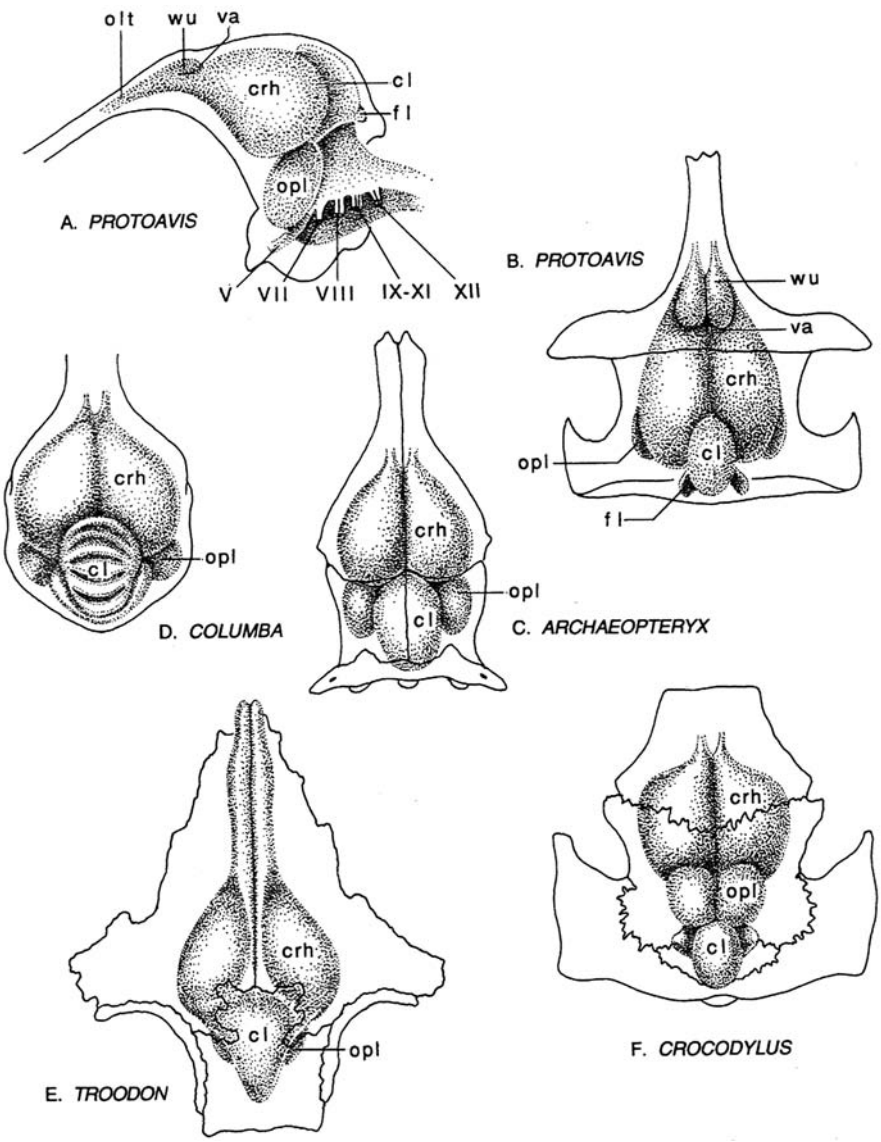


Figure 5.9. Comparative brain morphology of a crocodile (F), a nonavialan theropod (E), and birds (A–D); these fossil brains are reconstructed from endocasts (after Chatterjee 1997). A–B, *Protoavis*; note the development of large cerebral hemispheres, wulst, and vallecula, as well as displacement of the optic lobes ventrally and laterally, as in birds; the olfactory lobes are reduced considerably. C, *Archaeopteryx*; D, pigeon (*Columba*); E, *Troodon*; F, *Crocodylus*. Note the considerable brain enlargement and the rearrangement of the optic lobes in *Troodon* and birds relative to crocodiles. Abbreviations: cl, cerebellum; crh, cerebral hemisphere; fl, floccular lobe; olt, olfactory tract; opl, optic lobe; va, vallecula; wu, wulst; Roman numerals indicate the foramina for cranial nerves.

of relative brain size, refers to the special process wherein the brain expands more rapidly than would be expected from the growth of the rest of the body. Harry Jerison, a pioneer in paleoneurology, used endocasts to study in detail the encephalization process of extinct animals. In 1973, he synthesized his ideas in his seminal book, *Evolution of the Brain and Intelligence*. Jerison devised a method that compensates for the effect of body size, allowing independent comparisons of brain size among related groups. He used the ratio of actual brain weight to the expected weight as an estimate of relative brain size, which he termed the encephalization quotient (EQ). For reptiles,

especially nonavialan archosaurs, Jerison's encephalization quotient was

$$\text{EQ} = \text{brain weight} / 0.005 \times (\text{body weight})^{0.66},$$

whereas for higher vertebrates (birds and mammals) he estimated the encephalization quotient as

$$\text{EQ} = \text{brain weight} / 0.12 \times (\text{body weight})^{0.66}.$$

To determine the encephalization quotients for the extinct vertebrates, one must estimate both the brain size and the body size. The brain size is determined from the volume of the endocast, whereas the body size is inferred from the estimated model based on skeletal reconstruction. Using Jerison's method, I have estimated the EQs of selected species of pterosaurs, nonavialan dinosaurs, and birds. The selected data are plotted in figure 5.10A, superimposed on Jerison's "brain:body maps" for living reptiles and birds. The estimates of brain and body size of *Protoavis* give a relative brain size that falls entirely within the avialan polygon and is a clear departure from the reptilian level. By contrast, pterosaurs were clearly reptilian. The EQs of pterosaurs, nonavialan theropods, and birds are also plotted graphically in figure 5.10B for comparison. The estimated EQ value of *Protoavis* is 0.41, whereas that of *Archaeopteryx* is 0.34. The EQs of early birds fall within the lower range of living birds but lie well outside the range of nonavialan theropods and pterosaurs. Brain size increased greatly in the line of evolution toward birds as the cerebrum and cerebellum enlarged and increased in complexity.

I have calculated the EQs of many living birds (fig. 5.10B). Smaller birds (body weight of < 100 grams) in general have proportionately larger EQs (approximately equal to 1.0) than larger birds. In my survey, the crow is the intellectual elite, as its EQ approaches 1.6. The brain of crows, especially the forebrain, is significantly larger than that of any other birds, which is generally attributed to their cognitive abilities and intelligence. Their capability for social activities and tool-making is analogous to that of apes. The ostrich, on the other hand, is not so bright; it has a relatively small brain showing the lowest EQ (0.15). Most nonavialan terrestrial dinosaurs had brains no greater in relative size than those of crocodiles. Some nonavialan maniraptorans, such as *Troodon* (EQ = 0.25), began to show enlargement of brains. A similar trend of brain expansion is expected in other small Chinese maniraptorans, but I do not have any EQ data.

Arboreal Ecology and Brain Enlargement

It appears that early avialans such as *Protoavis* and *Archaeopteryx* possessed somewhat larger brains than those of pterosaurs and nonavialan terrestrial dinosaurs. What was the selection pressure that led to the astonishing cranial expansion of early birds? Jerison speculated that the evolution of birds from their reptilian contemporaries was the result of their invasion of a new adaptive zone—complex, three-dimensional, arboreal niches. He noticed that although both birds and pterosaurs developed the ability to fly, which demanded balance and coordination, the pterosaur brain was still reptilian in relative size, whereas birds were more encephalized. From this observation he argued that flight per se did not necessarily produce selection pressure toward avialan brain enlargement. The degrees of encephalization of two different aerial vertebrates may be related to their different styles of adaptation.

The pterosaurs habitually flew over shallow regions of the sea and fed on fish and other slippery animals. They lived in colonies on cliffs near seacoasts. Their activity was limited to a two-dimensional world, whether it was a vertical cliff or a horizontal expanse of water. The low EQs of pterosaurs may be correlated with their adaptation to a two-dimensional world, which is neurologically less demanding.

In contrast, the early birds, such as *Protoavis* and *Archaeopteryx*, inhabited woodland niches, most nearly like those of tree-dwelling primates, in a three-dimensional world. The judgment of distance is far more complex in this environment. The confusingly mottled background of leaves, branches, and other foliage at different levels of trees provided a strong selection pressure for enlargement of the brain to process complex three-dimensional audiovisual information. These early birds were depending more and more on sight and sound and less and less

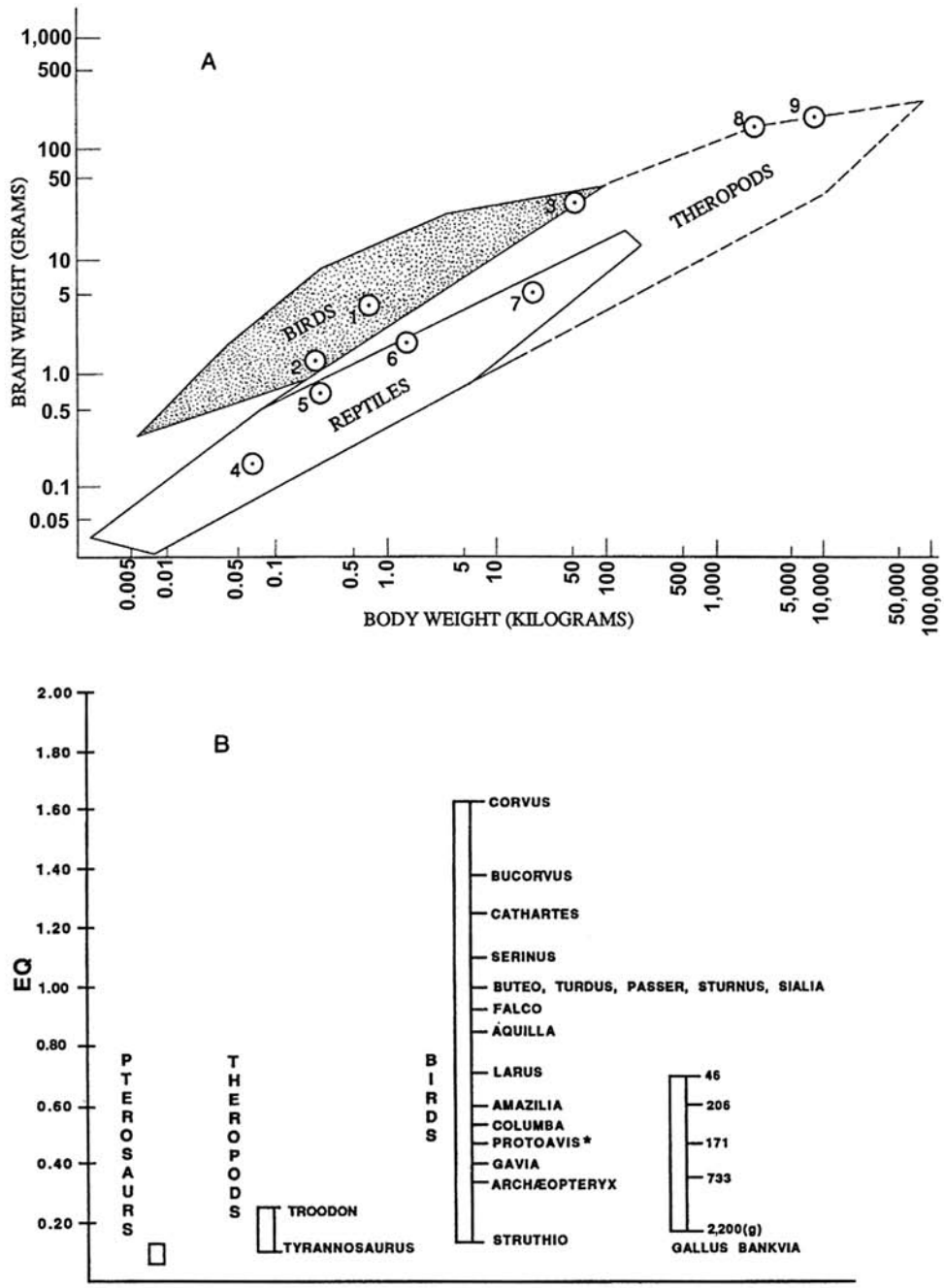


Figure 5.10. A, brain:body maps are the minimum complex polygons that can be drawn to enclose a set of points representing brain size plotted against body size (after Chatterjee 1997). Number points are for early birds (1, 2), nonavialan theropods (3, 8, 9), and pterosaurs (4, 5, 6, 7). 1, *Protoavis*; 2, *Archaeopteryx*; 3, *Troodon*; 4, *Pterodactylus*; 5, *Rhamphorhynchus*; 6, *Scaphognathus*; 7, *Pteranodon*; 8, *Allosaurus*; 9, *Tyrannosaurus*. The ratio of brain size to body size in early birds and Troodon falls within the avialan polygon, indicating considerable enlargement of the brain; the same ratio in pterosaurs and most nonavialan dinosaurs is in the reptilian domain. B, encephalization quotients (EQs) for pterosaurs, theropods, and birds. Except for coelurosaurs such as *Troodon*, dinosaur and pterosaur brains are generally small, in the reptilian range. The EQ values of *Archaeopteryx* and *Protoavis* lie in the lower range of living birds, whereas the EQ value of ostriches lies at the bottom. The right-hand bar shows that body weight is inversely correlated with EQs during ontogeny; the smaller the animal, the larger the relative brain size.

on smell. Life in the trees would have promoted the development of stereoscopic vision and hearing acuity, as well as the ability to orient in three-dimensional space. Jerison thus reasoned that the evolution of enhanced vision and hearing in woodland niches is the key factor for the sudden enlargement of the brain in early birds.

But why did the early birds adapt to arboreal life in the first place? There may be several reasons. First, arboreal habitat provided safer and more secure niches and conferred protection from the contemporary ground-dwelling reptiles. Second, trees were launching pads for early flights. Third, large flying insects, an almost untapped source of animal protein, may have been another stimulus toward the arboreal and aerial habitats of early birds.

Jerison believed that there is a general correspondence between relative brain size and intelligence. Intelligence is a quality of mental acuteness and comprehension unique to a species. It has a nonphysical as well as a physical reality, so it is hard to study. The brain is simply the organ that processes intelligence. Intelligence probably indicates adaptation to new environments, the ability to learn, and the capacity to create a perceptual world. Intelligence is related to the complexity of interactive behavior that can be studied and measured. Jim Hopson (1980), who has studied dinosaur brains, suggested that relative brain size might be linked to daily activity and thermoregulation. For example, most nonavialan dinosaurs had relatively small brains even by reptilian standards and were probably less active than are living endotherms. On the other hand, the very large brain of nonavialan coelurosaurs associated with cursorial adaptation and agility may indicate an endothermic level of activity. Hopson found a correlation between high EQ and endothermy. *Protoavis*, with an EQ close to 0.4, was probably metabolically as active as some living birds.

The Eye

The orbits are so large and deep in *Protoavis* that the right and left cavities nearly touch each other. The enormous size of the orbit, about one-third the length of the skull, clearly indicates a large eyeball, about 20 millimeters in diameter, which would provide larger and sharper images (fig. 5.4A). There is a prominent caudal vertical wall to support the large eye. Like most living birds, *Protoavis* must have been a visually oriented animal. It had not only large eyes but also well-developed optic lobes. Flying animals demand high resolving power for better perception of movements and for avoidance of collisions.

Walls (1963) has discussed the correlation between food habits (predator and prey species) and the position of the eyes in avialan skulls. In predatory birds such as hawks, eagles, and owls, the orbits are frontally placed, giving them excellent binocular vision. In prey species, on the other hand, the orbits are laterally placed, allowing the widest field of view to keep watch for impending danger. In *Protoavis*, the orbits are frontally placed with a large, overlapping field (fig. 5.11A). The snout is sharply tapered to clear its field of vision. John Pettigrew, an Australian neuroscientist, has worked on the position and significance of visual wulst in the forebrain region in living birds (Pettigrew 1979; Pettigrew and Frost 1985). In owls the wulst is highly developed, with a trigeminal bulge that may indicate stereopsis—highly precise, binocular depth perception. In *Protoavis*, we see the beginning of the development of a bulge on the wulst region (fig. 5.9B). The frontal position of the eyes, coupled with the development of bulging in the wulst, may indicate that *Protoavis* had achieved stereoscopic vision (fig. 5.11B). Stereoscopic vision would offer the possibility of some judgment of distance to help locate prey and insects more accurately. Pettigrew also noticed that the position of the vallecular groove relative to the olfactory bulbs is highly variable among recent birds and may be related to differences in feeding style and visual acuity. In *Protoavis*, the wulst is proximate to the olfactory bulb, as in some recent birds such as plovers (*Vanellus*) and bee-eaters (*Merops*), without any development of trigeminal expansion. This cerebral morphology indicates a visual feeding style rather than probe feeding.

The Ear

Protoavis had improved not only the visual but also the auditory system to supplement the sense of smell. The

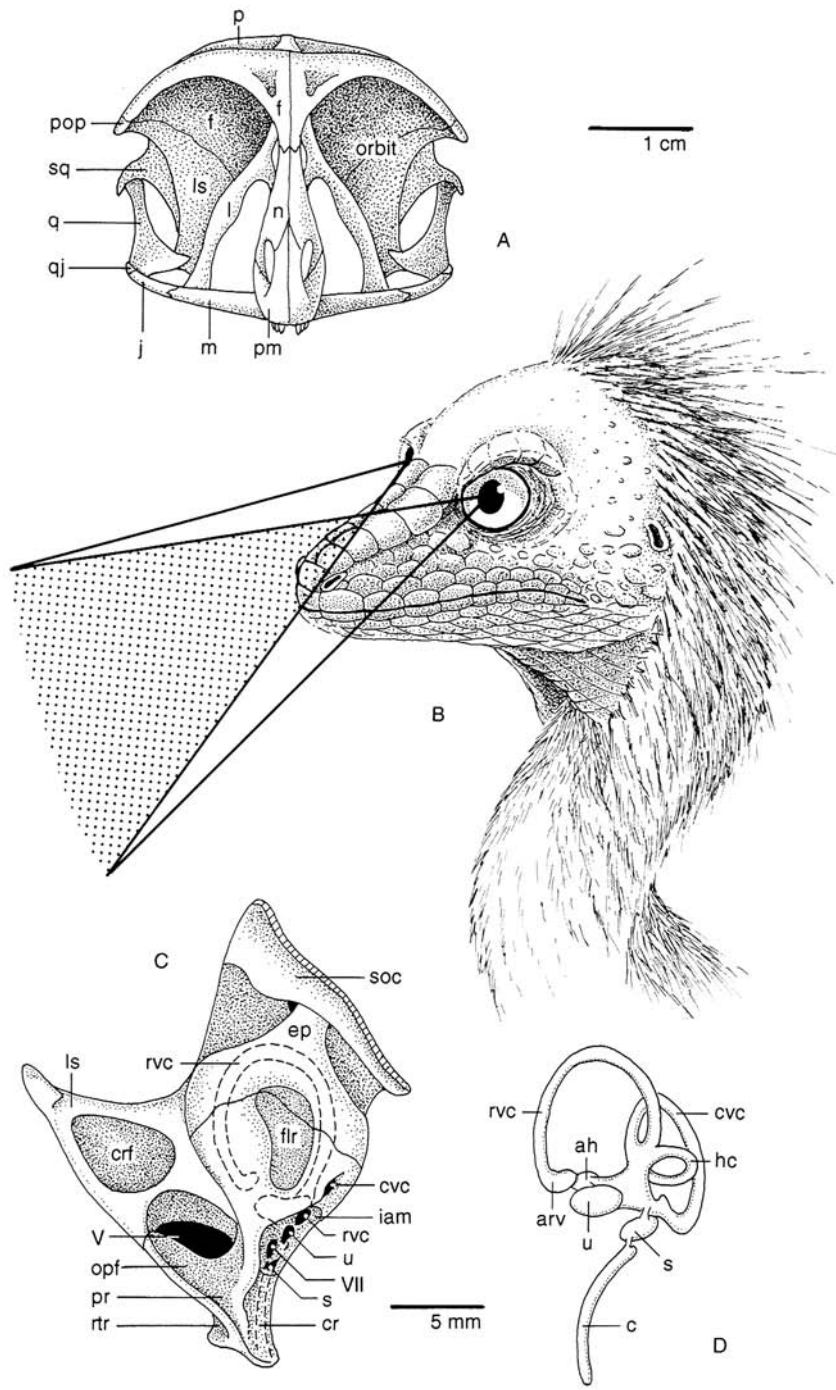


Figure 5.11. Reconstruction of the sense organs of *Protoavis* (after Chatterjee 1997). A, restoration of the skull of *Protoavis* in the cranial view to show the frontal position of the orbits and the stereoscopic view. B, life restoration of the head of Protoavis; with both eyes facing forward, *Protoavis* shows strong adaptations of stereoscopic vision, as in modern nocturnal birds of prey. C, internal view of the right side of the braincase showing the floccular recess (flr), the C-shaped bony tube for the rostral vertical canal (rvc), and the long tubular cochlear recess (cr). D, restoration of the inner ear of *Protoavis*. Abbreviations: arv, ampulla for the rostral vertical canal; c, cochlea; cvc, caudal vertical canal; hc, horizontal canal; rvc, rostral vertical canal; s, sacculus; u, utriculus; Roman numerals indicate the foramina for cranial nerves; for other abbreviations, see figures 5.4 and 5.5.

otic capsule was large, and spaces within it indicate that an elongate cochlea had evolved. This is the part of the inner ear that gives birds their keen sense of hearing. The middle ear region of *Protoavis*, as discussed earlier, is built in an avialan fashion. It shows two foramina, the fenestra ovalis for the reception of stapes in the front and the fenestra pseudorotunda behind (fig. 5.5A). The bony Eustachian tube leading from the tympanic cavity to the throat helps to equalize air pressure on both sides of the eardrum. The middle ear region is highly pneumatized where the rostral, dorsal, and caudal tympanic recesses can be seen (fig. 5.11C). The rostral tympanic recess shows contralateral communication. This feature is attributed to mechanisms of sound localization in birds. The tympanic recesses may have increased the sensitivity of the middle ear for detecting low-frequency sound.

The inner ear of *Protoavis* is reconstructed from the bony labyrinth and the cochlear recess (fig. 5.11D). On the medial surface of the braincase, the deep floccular recess is the most important landmark for the orientation of the canalicular system. An inflated bony tube around the floccular recess indicates the size and location of the rostral vertical semicircular canal. This is the longest part of the labyrinth. Two other semicircular canals, the caudal vertical and horizontal canals, are shared between the prootic and the opisthotic (fig. 5.11D).

The reception of auditory sensation is confined in birds to the papilla basilaris of lagena, which is elongated to form a bony tubular cochlear recess. This cochlear recess is well developed in *Protoavis* in the lower part of the prootic and opisthotic (fig. 5.11C). The elongated cochlea suggests the enhanced auditory reception of *Protoavis*, resulting in improved discrimination of sound frequency. In modern amphibians (frogs), reptiles (crocodiles, geckos), and birds, refined hearing is linked to vocalization. It is likely that *Protoavis* was vocal and presumably could hear its own voice for communication.

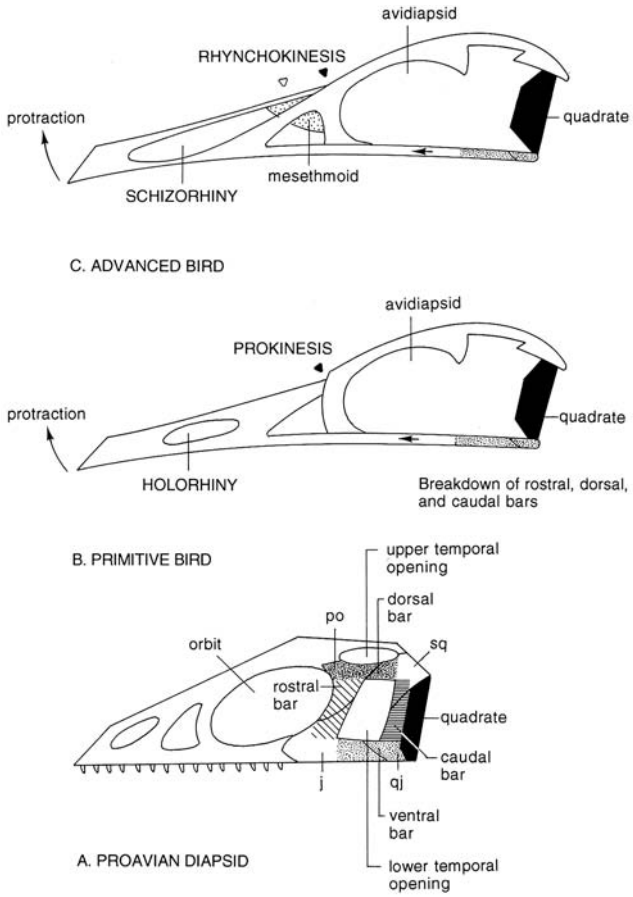


Figure 5.12. Evolution of the avian temporal region and cranial kinesis in response to streptostyly (after Chatterjee 1997). A, in proavian diapsids such as dromaeosaurs, the lower temporal opening is framed by four bony bars (rostral, dorsal, caudal, and ventral), which form a blocking device; as a result the quadrate cannot move forward. B, prokinetic birds with holorhinal nostrils acquired streptostyly and cranial kinesis by loss of the rostral (postorbital-jugal), dorsal (postorbital-squamosal), and caudal (squamosal-quadratojugal) bars; the quadrate becomes mobile and is able to raise the upper jaw as it is pushed forward. C, rhynchokinesis evolved after the loss of teeth from the premaxilla-maxilla bar, the development of the schizorhinal nostril, and forward extension of the mesethmoid under the dorsal bar; the solid pointer indicates the craniofacial hinge; the open pointer indicates the additional bending axis on the dorsal bar in rhynchokinesis.

Cranial Kinesis

Major features that differentiate avian skulls from those of nonavian theropods such as dromaeosaurs are modifications in the temporal region concomitant with the development of cranial kinesis (see chapter 15). In dromaeosaurs, the diapsid arches are intact (fig. 5.12A). In birds, three diapsid arches surrounding the lower temporal opening (the dorsal, ventral, and caudal bars) are eliminated so that the quadrate becomes streptostylic (fig.

5.12B). Cranial kinesis allows birds to move the upper jaw with respect to the braincase. In modern birds, two main types of kinesis are recognized relative to the position of the dorsal line of flexure and the nature of nasal opening. In prokinesis, bending occurs at a single transverse axis across the frontonasal hinge, so that the entire upper jaw moves as a unit. Prokinesis is associated with a holorhinal naris (the posterior outline of the opening is fairly rounded), which makes deformation within the upper jaw impossible (fig. 5.11B). In rhynchokinesis, the dorsal flexion zone of the upper jaw has been displaced forward so that its rostral part can be moved. The location, number, and extent of the hinges on the dorsal bar characterize different forms of rhynchokinesis. Rhynchokinesis is generally associated with a schizorhinal naris (the posterior margin of the opening forms a deep slit) (fig. 5.12C). Prokinesis is a primitive adaptation, whereas rhynchokinesis is a derived feature.

The movement of the quadrate powers cranial kinesis. In birds, the quadrate can move in a variety of directions relative to the braincase. In streptostyly the quadrate swings forward and backward. In opisthostyly the quadrate moves only caudally from its resting position (fig. 5.13A–B). In parastyly the quadrate moves in a transverse direction (Chatterjee 1991).

In *Protoavis* we see the beginning of the development of kinesis. Like modern birds, *Protoavis* has lost the rostral, dorsal, and caudal arcades of the lower temporal opening, as well as the ectopterygoid, making the jugal bar, quadrate, and pterygoid mobile (fig. 5.13C–D). The ventral end of the lacrimal has developed a sliding joint with the jugal bar. Both the quadratojugal and the quadrate ramus of the pterygoid have minimized contacts with the quadrate to enhance mobility. These articulations form pin joints restricted to the foot of the quadrate. The orbital process in *Protoavis* serves as an effective lever arm for the protractor quadrate muscle. The spherical head of the quadrate fits into a concavity of the squamosal to form a ball-and-socket joint, allowing the quadrate to swing freely in any direction.

Like modern birds, *Protoavis* has four functional units and four principal joints on each side of the skull (fig. 5.13E). The functional units are (1) the upper jaw, (2) the jugal bar + the pterygoid-palatine bar, (3) the quadrate, and (4) the braincase. These four units form a four-bar crank chain on four joints. These flexible joints are (1) quadrate head-squamosal; (2) quadrate-quadratojugal; (3) quadrate-pterygoid; and (4) frontal-nasal. If the braincase is held stationary and the quadrates are swung forward, the upper jaw is raised at the fronto-nasal joint. The upper jaw is the mobile unit for procuring food, whereas the braincase is the stationary unit for housing neurosensory organs. These two units are joined by various links. The quadrate is the vertical link and the main crank device. Its head forms a fulcrum on the undersurface of the squamosal and moves forward and backward at its foot so that the force can be transmitted to the beak through a pair of horizontal links (fig. 5.13E). The jugal bar forms the lateral link, whereas the pterygoid-palatine bar acts as the median link. The quadrate is flexibly attached by pin joints to these horizontal links on either side of its foot. Because the jugal bar and the pterygoid-palatine bar share a similar mechanical function, as a push rod between the upper jaw and the quadrate, they are considered functionally as a single link to simplify the model. There are three flexible or bending zones that permit movement of the upper jaw. The dorsal bending zone lies between the nasal and frontal bones, the lateral bending zone is between the maxilla and jugal, and the palatal bending zone occurs across the vomer-palatine contact. In modern birds, the bending zones become very thin and pliable with the fusion of skull bones. In *Protoavis*, these zones are connected by thin and flexible joints (Chatterjee 1991). It appears that a primitive form of kinesis might have developed in *Protoavis*.

Two pairs of muscles act together to raise the upper jaw and depress the lower jaw (fig. 5.13C–D). The orbital process of the quadrate acts as a lever arm for the *M. protractor pterygoidei et quadrati* muscle. The action of the muscle is to pull the quadrate forward. As the quadrate foot moves forward, this force is imparted to the jugal bar, which, in turn, pushes the upper jaw forward. Since the upper jaw is flexibly attached at the bending zones, the forward push of the jugal bar rotates the upper jaw

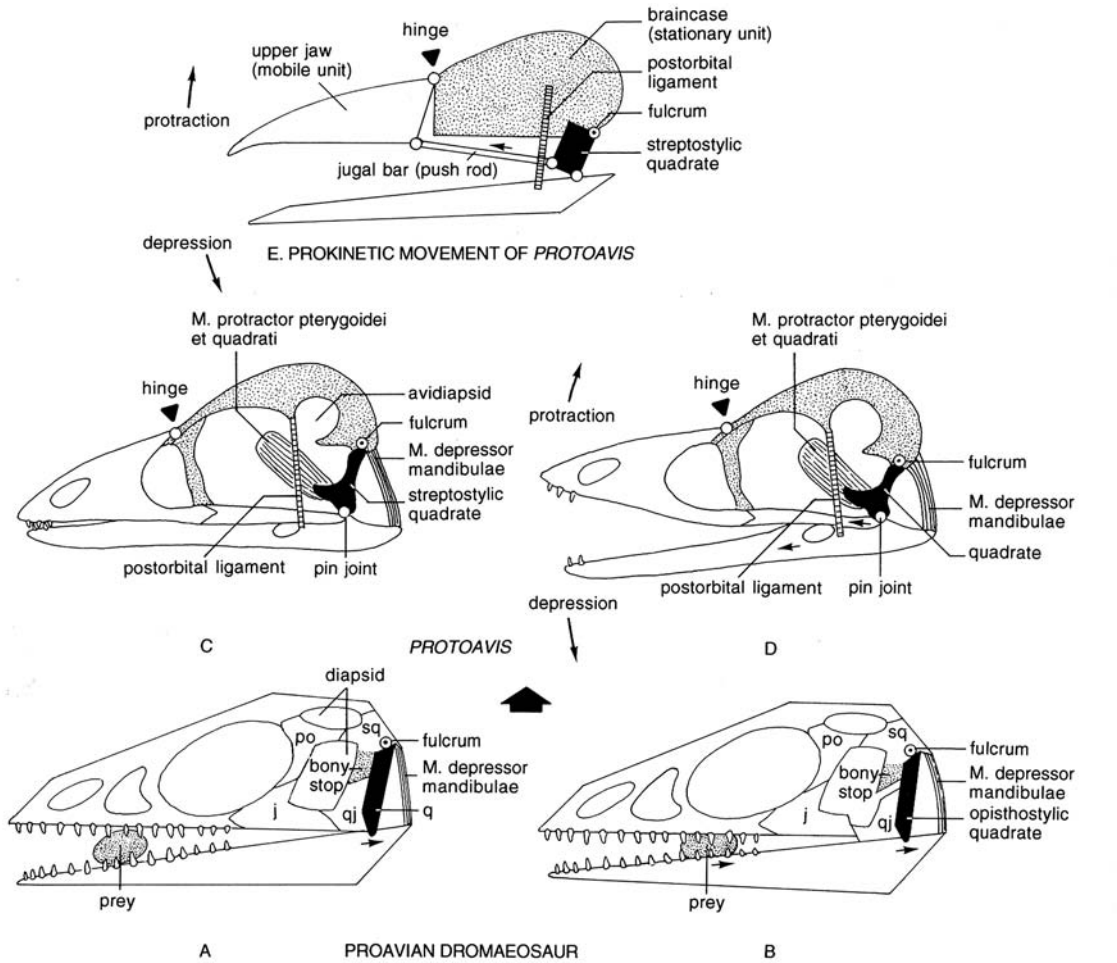


Figure 5.13. Evolution of cranial kinesis in birds (after Chatterjee 1997). A and B, in a maniraptoran dromaeosaur the quadrate head has developed a ball-and-socket joint with the squamosal. The quadrate cannot move forward because of the blocking action of the squamosal-quadratojugal bar in front of the quadrate, which prevents streptostyly. However, the combined quadratojugal-quadrate can move backward (opisthostyly), which, in turn, would permit caudal movement of the lower jaw relative to the skull during the bite; this backward movement of the jaw during prey capture would assist in slicing and shifting the flesh back toward the throat, ready for swallowing. C, in *Protoavis*, with the acquisition of an avidiapsid condition (i.e., confluence of the orbit with the two temporal fenestrae), the squamosal-quadratojugal bar in front of the quadrate is eliminated, and a pin joint is developed between the quadratojugal and the quadrate. The quadrate becomes streptostylic and can move forward and backward. D, during contraction of the depressor mandibulae muscle, the foot of the quadrate moves forward; this rotates the upper jaw dorsally. The elevation of the upper jaw and the depression of the lower jaw are coupled by the postorbital ligament (Bock 1964). E, functional interpretation of prokinesis in the skull of *Protoavis*, based on the four-bar crank mechanism. The skull has four functional units and four principal joints on each side of the skull. The braincase is the stationary unit. As the jaw is depressed, the quadrate is swung forward and the upper jaw is raised. Cranial kinesis allows a larger gape to facilitate high intake of food.

dorsally. Bock (2003) concurred that a primitive form of avialan kinesis has already developed in *Protoavis*.

Kinesis in birds increases the gape to allow a high intake of food. It also allows sophisticated manipulation of food in the mouth. Prokinesis is not possible among nonavialan dinosaurs because of the presence of the squamosal-quadratojugal bar, which acts as a blocking device for streptostyly (fig. 5.12A). In birds, when the jaws are closed, further opisthostylic quadrate movement creates a wedge that opens backward in the mouth, thus

preventing food from escaping. This opisthostylic quadrate movement also allows the upper and lower jaws to close quickly (fig. 5.13D). Opisthostyly is a primitive feature and is developed in small nonavialan theropods, such as ceratosaurs and coelurosaurs, to allow more efficient capture of food and to push prey back toward the throat, ready for swallowing (fig. 5.13A–B). In some birds, when the jaw is lowered, the quadrate moves sideways (parastyly), which, in turn, moves the caudal part of the lower jaw sideways. This lateral spreading of the lower jaw increases the diameter of the throat, which helps when swallowing large pieces of food. Parastyly is common among large theropods (i.e., allosaurs and tyrannosaurs), where lateral mandibular spreading occurs along a vertical flexible joint between the dentary and postdentary bones. The evolution of cranial kinesis in birds is discussed in chapter 15.

Mode of Life

The adult *Protoavis*, as restored from available skeletal material, is a small, gracile bird, about the size of a pheasant (*Phasianus*), with a long bony tail (fig. 5.14). The skull is attached to an elongated, S-shaped neck. The trunk is short, the girdles are robust, and the limbs are well built for locomotion. The estimated overall length is 60 centimeters, which is comparable to that of the Solnhofen specimen of *Archaeopteryx*. *Protoavis* is relatively strongly built, like predatory birds. Its estimated weight is about 600 grams—about the size of *Archaeopteryx*.

Protoavis lived in the tropics of Texas mainly in trees. It was probably a predatory bird, which is indicated by the carnivorous teeth at the tip of the jaws. Three small teeth are present in the maxilla and two in the dentary; the posterior parts of the jaws were edentulous. The brain itself became relatively larger than that of the contemporary dinosaurs and more elaborate in design. The outstanding feature of the skull is the relocation of the enormous orbits to the front (fig. 5.8B). The eyes were set in bony cups that held them separate from the brain. The earliest birds probably survived as small, nocturnal animals to avoid direct interaction with their diurnal reptilian contemporaries. To locate food in the hazardous three-dimensional world of the trees, they developed sharp eyes in preference to keen noses. Heterocoelous neck vertebrae permitted a wide range of motion of the head in the performance of these tasks. The jaws acquired kineticism to increase gape and facilitate a high intake of food. *Protoavis* acquired hearing acuity that might be associated with vocal sounds for communication. In woodland and forest environments, where it might be difficult to see, sounds might be an effective way of mediating social interactions. Its claw morphology shows that *Protoavis* could climb trees. A tree would have been used in many ways by early birds—as an escape refuge, as a hiding place, as a nesting site, or as a resting site. Like modern birds, *Protoavis* probably lived in a complex habitat, spending some time feeding on the ground but using trees for hunting, sleeping at night, and nesting.

Like modern birds, *Protoavis* acquired two independent and specialized methods of locomotion: flying with the forelimbs and walking with the hindlimbs. *Protoavis* was an obligatory biped, and the forelimbs played no role in supporting weight. Maintaining proper balance on two legs for support and locomotion was a major innovation in nonavialan theropods. Many of these bipedal hallmarks persisted in early birds. For example, the hip joint was adapted to an erect posture with perforation of the acetabulum and a completely inturned head. The hindlimbs are slender but strongly built and show features of cursorial adaptation. The distal segments of the hindlimb became longer than the proximal ones to increase stride length and enhance speed. The metatarsals are elongated and closely bound together. The mesotarsal ankle joint suggests digitigrade posture. *Protoavis* walked on its digits, with the heel and anklebones carried off the ground. The fifth digit was lost. The reversed hallux forms a prop to support the digitigrade pes.

The increase in the area of the pelvic girdle, the backward rotation of the pubis, and the reduction of the tail indicate a subtle change in the posture of early birds from the dromaeosaurid design. The principal effect of this reorganization of pelvis and tail would be to shift the center

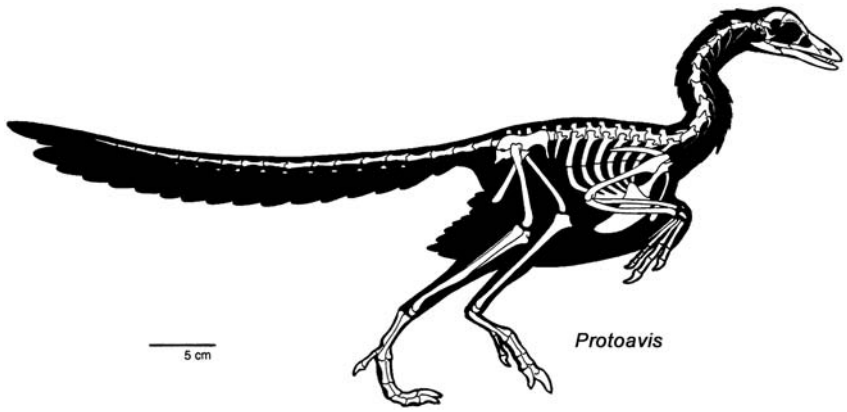


Figure 5.14. Skeletal restoration of *Protoavis texensis* (after Chatterjee 1997). In life, the adult *Protoavis* would be approximately the size of a pheasant (*Phasianus*), 60 centimeters in length, if its long bony tail is taken into account.

of gravity forward. In nonavialan theropods, the femur rotated back and forth considerably at the hip joint for propulsion. In *Protoavis*, the leg bones were held in a Z configuration, as in modern birds. In this position the femur was kept subhorizontally and its distal end moved up and down slightly. The main functional movement was transferred to the knee joint, where the tibia swung forward and backward. Several osteological features suggest this new posture in *Protoavis*. The preacetabular process of the ilium was elongated cranially and provided a large area for the attachment of the iliotibialis cranialis muscle. This muscle would protract the femur in the subhorizontal position. With the development of the cranial prolongation of the ilium, the pubis was relieved of its role in femoral protraction and could rotate backward. The principal femoral retractor, the caudofemoral longus muscle, was considerably reduced, as is evident from the loss of the fourth trochanter and the truncation of the tail (Gatesy 1990). The tail, an important balancing organ in dromaeosaurs, was considerably reduced in *Protoavis*. To counterbalance the long tail, the pubis was rotated backward so that heavy viscera could be shifted caudally under the pelvis and over the legs. The ischium and pubis became open ventrally to make room for the viscera. With the development of the subhorizontal attitude of the femur, the center of gravity was positioned near the distal end of the femur. The tibia now played a major role in propulsion, and the knee joint showed greater motion than the hip joint. The development of both cranial and later cnemial crests in *Protoavis* may reflect their important role in knee movement.

The small size of *Protoavis* confers favorable weight-surface relationships for flight, allowing a bird to move through the air with smaller wings and at lower airspeed. *Protoavis* shows many derived features associated with flapping flight that are not encountered in *Archaeopteryx*. Of particular importance are the keeled sternum, the hypocleidium-bearing furcula, the strut-like coracoid, large flight muscles, and the triosseal canal for the supracoracoideus tendon (fig. 5.15). The glenoid cavity faces dorsolaterally, which permits unrestricted movements of the humerus in all directions. The humerus is an exceptionally strong bone and shows all the bumps and ridges for the attachment of the flight muscles. The specialized linkage system of elbow and wrist joints would stiffen the entire extended wing into a plane to resist twisting when exposed to air pressure during flight. The presence of feathers is inferred indirectly from the development of quill knobs in the hand. The furcula and the keeled sternum must have accommodated large flight muscles. The flexible furcula would act as a spring between the shoulder joints during the flight strokes. The presence of a triosseal canal suggests that the supracoracoideus muscle must have functioned effectively as a wing eleva-

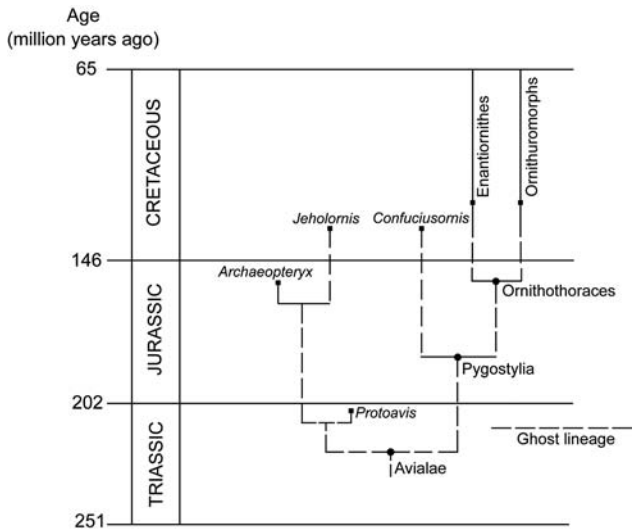


Figure 5.15. Ghost lineages of early birds suggest that the common ancestor of all bird lineages converge back in time to the Late Triassic, a view consistent with the presence of *Protoavis*.

tor and that the animal could possibly have taken off from the ground. The enlargement and partial fusion of pelvic bones, a relatively short horizontal femur with an antitrochanter articulation, and a mesotarsal ankle joint all may indicate that the hindlimb was modified as a landing gear.

The elbow and wrist joints of *Protoavis* were coupled automatically without much muscular effort and were restricted to a single plane, as in modern birds. This complex linkage system between elbow and wrist joint is central to the normal functioning of the avialan wing, not only in its folding and unfolding but also in maintaining the proper position of the skeletal elements during flight. *Protoavis*, however, did not achieve the strength, rigidity, and reinforcement that are required to withstand the strain imposed by sustained flight. Rick Vasquez (1992, 1994) discussed in detail the complex wrist movements during the flapping flight of modern birds. The wrist bones of *Protoavis* show some interesting though primitive morphology, which may provide clues to the early evolution of flapping flight. The radiale is very pronounced and would lock the manus in the extended position. This mechanism prevents the manus from supinating during gliding or maneuvering. Vasquez noticed that in modern birds the ulnare is a large, complex bone that interlocks with the ulna and the ventral ridge of metacarpal III. This arrangement prevents the manus from hyperpronating during the downstroke. In *Protoavis*, the ulnare is a small, spherical bone that articulates with a ventral ridge of metacarpal III but lacks the complex interlocking device known in modern birds. It is doubtful that such a small ulnare in *Protoavis* could prevent the manus from hyperpronating during slow, maneuvering flight. In all probability, *Protoavis* was designed for powered flight for a short distance at a cruising speed, although essentially a glider. As in *Archaeopteryx*, the long tail of *Protoavis* provided stability and enabled it to control its motion with respect to pitch and roll. The animal probably kept a straight and level course without much turning, climbing, or diving. Cruising flight is more primitive and less strenuous than slow flight. With further improvement of the wrist, fusion of the skeleton at critical joints, and loss of the tail in Cretaceous birds, more sophisticated flight evolved.

Given its earliest avialan record, *Protoavis* shows a mosaic evolution, including primitive hindlimbs and hands but a highly derived skull, pectoral girdle, and pelvic girdle that are comparable to those of ornithurine birds. The assortment of primitive and advanced characters in *Protoavis* reveals the example of a modular evolution during the emergence of a major clade where key evolutionary changes tend to take place in different rates in different body units, not all at once. Chiappe (1996) concluded that evolution of modern flight apparatus preceded the evolution of the modern bird mechanism of terrestrial locomotion. In other words, modification of the forelimbs would have already occurred in the early evolution of birds, while many modifications of hindlimbs for refined terrestrial locomotion lagged behind. Zhang et al. (2008) noticed similar changes in locomotor module in early Chinese birds with much derived pectoral girdles and forelimbs and very primitive hindlimbs and tails. In other words, early birds first developed flight capability and then became modern in the features of the hindlimbs and the tail.

Dockum Paleoecology

The Dockum sediments and fossils give some idea of the environment. In Triassic time, Texas was situated close to the equator, with a climate that was warm, probably mostly wet, and dominated by monsoonal circulation (fig. 5.1). The distribution of detrital zircon suggests that a large Mississippi-scale paleoriver—the Chinle-Dockum River—was flowing primarily northwest from western Texas to eastern Nevada, supplied by water from the Amarillo-Wichita Uplift (Riggs et al. 1996). The river fluctuated in size over time; its environs ranged from forest to woodland, and the region was dotted with lakes and ponds.

Plant fossils are excellent indicators of past climate, but the flora from the Dockum sediments is poorly known. Sidney Ash (1972), a paleobotanist who has identified many plant fossils from the contemporary Petrified Forest of Arizona, also looked at the Dockum flora. He was able to recognize several common plant fossils, including the remains of three ferns (*Cynepteris*, *Phlebopteris*, and *Clathropteris*), five gymnosperms (*Pelourdea*, *Araucarioxylon*, *Woodworthia*, *Otozamites*, and *Dinophyton*), and one possible cycad (*Sanmiguelia*). The logs of conifer trees such as *Araucarioxylon* are common in the Dockum. Some of these trees were 40 to 50 meters tall. The rarity of plant fossils in the Dockum red beds is due to the oxidizing environment that destroyed most of their remains. In rare instances, I have encountered beautiful leaf impressions, petrified wood, and lignite layers, as well as conchostracans (small aquatic crustaceans) in green mudstone facies that may represent reducing pond deposits.

From the remains of the Dockum flora, Ash concluded that the climate was moist and warm. He argued that the living relatives of the Dockum ferns and gymnosperms now mostly inhabit humid tropical areas and that the large specimens of *Araucarioxylon* suggest an abundant water supply. The pollen assemblages demonstrate that a moderately diverse flora was present in the Dockum environments and that the climate was moist. There were three distinct plant communities in the Dockum: (1) a flood plain swamp community of ferns and cycads, (2) a lowland closed canopy of forest of *Araucarioxylon*, and (3) an upland gymnosperm community. These plants supplied the food and camouflage for the Dockum herbivores, including forms such as aetosaurs, trilophosaurs, dicynodonts, and toothless *Shuvosaurus*.

The Dockum fauna gives us further clues about the Late Triassic environment. The locally abundant aquatic animals, such as bivalves, conchostracans, fish, metoposaurs, and phytosaurs, support the presence of large bodies of water. Within the Dockum ecosystems, three principal habitat subzones for the vertebrates have been identified: (1) aquatic—rivers, lakes, and ponds inhabited by fish, metoposaurs, and phytosaurs; (2) lowland—margins of rivers, lakes, and ponds occupied by the brachyopids, rhynchosaurs, protorosaurs, trilophosaurs, and squamates; and (3) upland—divides between two streams, interfluves, populated by aetosaurs, rauisuchians, dinosaurs, and therapsids.

In the Dockum terrestrial communities, two major groups of archosaurs thrived: the crurotarsans and the early dinosaurs. When the dinosaurs first appeared on the Triassic scene, they were relatively small, overshadowed by the crurotarsans. Some of the Triassic crurotarsans show stunning convergences with later dinosaurs. For example, aetosaurs show ankylosaur-like body armor and limb structures, whereas *Postosuchus* exhibits theropod-like posture and carnivorous adaptations. Similarly, *Shuvosaurus*, another crurotarsan, is surprisingly similar to ostrich dinosaurs in size, proportion, and inferred activities. These superficial similarities indicate that the Triassic crurotarsans had nearly identical functional requirements and thus evolved structural adaptations similar to those of later dinosaurs. These animals lived in a dense riverine forest of conifer trees with an understory of ferns that formed the base of the terrestrial ecosystems. The Dockum food chain started with the plant-eating animals and progressed through a series of larger carnivorous animals. Surprisingly, at the top of the food chain was the rauisuchian *Postosuchus*. Evolution and resource availability played major roles in the formation of the Dockum

community. A diverse variety of food was abundant in the Dockum environment, allowing an array of different types of animals to coexist with little interference (Chatterjee 1985, 1992a).

Although both birds and nonavialan dinosaurs appeared simultaneously during the latter part of the Triassic and coexisted throughout the Mesozoic, they adapted different strategies and explored different niches for obtaining food and shelter. Nonavialan dinosaurs tended toward large to gigantic body size in a terrestrial habitat and became the dominant land animals in the Jurassic and Cretaceous periods. Unlike birds, all nonavialan dinosaurs disappeared at the end of the Cretaceous calamity. Birds maintained a small body size because of their flight constraints and exploited a wide range of ecological niches beyond the reach of nonavialan dinosaurs. They survived two major mass extinctions in the Mesozoic and enjoyed bursts of adaptive radiation during the Tertiary. In living birds you can hear the distant murmurs of a pioneer Texan dinosaur who ventured into a new frontier to conquer the sky about 225 million years ago.

Controversy over *Protoavis*

From the beginning, *Protoavis* was received with much skepticism, and this is to be expected whenever a fossil with such important implications is discovered, which predates *Archaeopteryx* by some 75 million years and pushes the origin of birds back to the dawn of the age of dinosaurs. Moreover, the specimens were largely disarticulated. If *Protoavis* is indeed a bird, then its significance and implications are enormous in avialan biology. It is by far the oldest bird, unseating *Archaeopteryx* from its venerable position as Urvogel. *Protoavis* has more defining avialan features than *Archaeopteryx*. The current consensus about the origin of birds, often called the theropod hypothesis, states that birds are deeply nested within maniraptoran theropods (Ostrom 1976a; Gauthier 1986). The find of a Triassic bird creates a perpetual conundrum in paleontology, called a "temporal paradox," because maniraptoran theropods, the ancestors of birds, have been found in rocks younger than those containing *Protoavis* or *Archaeopteryx*. The temporal position of *Protoavis* would imply very early divergence of major clades of theropods by the Late Triassic time. The fossil record of maniraptorans in younger sediments has been interpreted as inconsistent with *Protoavis* (Chiappe 1996; Witmer 2002). However, recent discovery of the oldest definite record of a manirapproran theropod from the Early Jurassic Lufeng Group of China is closing most of the temporal gaps between *Protoavis* and their putative ancestors (Zhao and Xu 1998). It contradicts the theory that nonavialan maniraptorans occur too late in the fossil record to be related to *Protoavis*. Recent discovery of an associated skeleton of a miniature bird-like maniraptoran from the Post quarry where *Protoavis* skeletons were recovered closes the temporal and morphological gaps between *Protoavis* and its immediate maniraptoran ancestor. Moreover, in cladistic phylogeny, the immediate goal is to identify the closest sister taxon of birds rather than ancestors.

There is a wide range of opinions about the affinity of *Protoavis*. Most criticisms leveled against *Protoavis* are restricted to the fragmentary and disarticulated nature of the material and interpretation of some of the elements; these critics have acknowledged that some bones in the skull (loss of the postorbital bone, a streptostylic quadrate with an orbital process), the highly inflated braincase, or the heterocoelous neck vertebrae show distinct avialan attributes, while the hindlimbs are theropod-like, but they are reluctant to call the Triassic animal a certified bird (Ostrom 1991b; Witmer 2001, 2002; Chiappe 1995a, 2007). In contrast to their agnostic attitudes, some ornithologists and neuroanatomists offered the strongest endorsements of *Protoavis* as the earliest bird, or Urvogel (Allman 1999; Martin 1988; Tarsitano 1991; Bock 1998; Peters 1994; Kurochkin 1995; Starck and Ricklefs 1998; Feduccia 2012). Currie and Zhao (1993, 2244) regarded the braincase of *Protoavis* to be "amazingly similar" to that of *Troodon*, the Cretaceous maniraptoran, which is close to the ancestry of early birds, in the development of a large floccular recess, cranial pneumatic recesses, a metotic strut, and the occipital opening of the vagus canal—an assessment endorsed by Witmer (2001). This avialan affinity of *Protoavis* was supported by independent cladistic analysis (Dyke and Thorley 1998). The combination of

derived forelimbs with primitive hindlimbs in *Protoavis* fits the general trend of the modular evolution of locomotion in early Chinese birds (Zhang et al. 2008). Chiappe (1996) concluded that the evolution of modern flight apparatus preceded the evolution of the modern bird mechanism of terrestrial locomotion.

The irony of paleontological discovery has always been that as a new transitional fossil is discovered, it becomes highly controversial, whether the first fish, first tetrapod, first reptile, first bird, first mammal, or first human; its phylogenetic position swings back and forth between the two linking groups. *Archaeopteryx* has weathered many challenges, demoted to reptiles first, then enjoying its avialan glory for more than a century, recently back to its theropod roots, but regains marginally its avialan status.

Some critics dismissed the fossils of *Protoavis* as being a chimera, that is, a death assemblage of different animals instead of associated parts of a single kind of animal (Ostrom 1991b; Dingus and Rowe 1998). For example, Renesto (2000) made the very tentative suggestion that the cervical vertebrae of *Protoavis* may resemble those of Italian drepanosaurs such as *Megalancosaurus* in lateral and ventral views. However, he acknowledged that the centra of *Megalancosaurus* were procoelous, whereas in *Protoavis* they are heterocoelous. Moreover, *Megalancosaurus* material is crushed two-dimensionally, obscuring most features and making the comparison problematic. I have collected dozens of *Megalancosaurus*-like vertebrae, which are preserved in three-dimensions. None shows heterocoelous centra. Moreover, I did not find any sign of intermixing of other Dockum vertebrates in the taphonomy of the *Protoavis* skeletons in the Post quarry; the bird fossils were found in a block of mudstone tightly clustered, which lay about 1 meter above the actual bone bed; the *Protoavis*-bearing layer was virtually sterile without any trace of other Dockum vertebrates, large or small (Chatterjee 1991). Evgeny Kurochkin (1995, 49), who studied the original specimens, forcefully stated that it "is impossible to suggest that this is a mixed collection of different vertebrates." Even if the chimera hypothesis is found to be true, this does not discount the possibility that at least some of the material might indeed be avialan (Witmer 1991). Similarly, Walter Bock (1998, 808), who examined the *Protoavis* fossils, noted, "If one was being severely critical, few features are conclusively avialan." In spite of acrimonious debate, I concur with some critics that until better and articulated material of *Protoavis* is discovered in the future, its phylogenetic position will remain murky.

When I first described *Protoavis* (Chatterjee 1991), I mentioned that *Protoavis* material came from two quarries: the partial associated skeletons came from the Post quarry in Garza County (the Cooper Canyon Formation), and the disarticulated elements were recovered from the Kirkpatrick quarry in Crosby County (the Tecovas Formation). Some critics have pointed out that the material came from two horizons of the Dockum Group and may belong to two different taxa. However, recent detailed mapping by my students, Jeff Martz and Bill Mueller, suggests that both these quarries occur in the Tecovas Formation of Carnian age.

However, the discovery of a Triassic bird is not totally surprising. More than a century ago, the Yale paleontologist Othniel Charles Marsh (1880) cogently argued that three Mesozoic taxa, *Archaeopteryx*, *Hesperornis*, and *Ichthyornis*, differ so widely from one another that the evolution of birds must have taken place at a much earlier time, perhaps at the end of the Triassic. He predicted that Triassic birds with a freely movable quadrate bone would be found to fill the major morphological and evolutionary gaps in avialan history. *Protoavis* approaches the predicted structure and size of the ancestral bird envisioned by Marsh. Similarly, the prolific radiation of birds in the Early Cretaceous of China clearly indicates that their origin must have commenced much earlier, possibly in the Triassic.

Several independent lines of evidence support the existence of a Triassic bird: molecular phylogeny, footprints, bone histology, and ghost lineages. During the past four decades, the molecular clock hypothesis has provided an invaluable tool for building evolutionary time scales and tracking the temporal diversification of clades. It is a technique in molecular evolution that uses fossil constraints and rates of molecular change to deduce the time in geologic history when two other taxa diverged. It sheds new light on the timing of the origin

of birds. Birds are generally regarded as the closest extant relatives of crocodilians, owing to some unique archosaurian features such as an ossified laterosphenoid, an antorbital fenestra, and a mandibular fenestra, which are shared between two groups. The divergence of birds and mammals provides a reliable calibration point on which to anchor other molecular clocks of Mesozoic vertebrates. Using the mitochondrial and nuclear genome, the divergence between the avialan and crocodilian lineages probably took place around 240 million years ago at the base of the Triassic period, slightly earlier than *Protoavis*, the earliest fossil suggests (Janke and Aranson 1997; Kumar and Hedges 1998). Thus the presence of a Triassic bird is consistent with molecular evidence.

More supporting evidence comes from bird footprints. Tridactyl bird tracks have been found from the Late Triassic Manassas Sandstone in the Culpepper Basin of Virginia, which were probably left by *Protoavis*-like animals (Weems and Kimmel 1993). Such avialan footprints from Virginia would push the origin of avialans back to the time of *Protoavis*.

The bone histology of *Protoavis* suggests its avialan affinity. Anusuya Chinsamy (personal communication) studied three femora of *Protoavis* from the Kirkpatrick quarry (TTU P 9271–9373) for paleohistological study. She found the bone microstructure of *Protoavis* is similar to that of enatiornithine birds and concluded:

> The femora of *Protoavis* combine a bird-like morphology of the lateral condyle, thin-walled bone shafts, and specific histological similarities to basal birds. The wall thickness is about 17% of the diameter, which compares well with that of (noneuornithurine) *Patagopteryx* (18.5%) and the Enantiornithes (13.7%). The bone microstructure is composed essentially of parallel-fibered bone with several lines of arrested growth (LAGs). Limb bones composed exclusively of the slow growing parallel-fibered bone are exceptional among both avialan and nonavialan theropods and have hitherto been recorded only in adult Enantiornithes, although parallel-fibered bone is amply deposited in some Mesozoic birds as well. LAGs are present in the compacta of the Enantiornithes and all other basal (nonornithurine) birds. No channels for blood vessels and connective tissue occur in the compacta, but as in Enantiornithes, the enlarged osteocyte lacunae with hyper-ramified canaliculi are present in TTU P 9373.

There are major gaps in the fossil record of Mesozoic birds. We know that many members of the group were around during the different periods of the Mesozoic, but the fossil record of birds is notoriously poor before Early Cretaceous Jehol biota, when several clades of birds—avialans, pygostylians, enatiornithines, and ornithuromorphs—suddenly appeared. All the ancestors of avialan clades reported in Jehol must have appeared much earlier than the Early Cretaceous, but their fossil record is still lacking. Several bird-like fossils such as *Xiaotingia*, *Anchiornis*, and *Aurornis* have been recently found from the Middle to Late Jurassic Tiaojishan Formation of China, indicating their early radiation. In spite of lack of fossils, it is likely from the radiation of bird-like fossils in the Late Jurassic and Early Cretaceous of China that the origin of birds could be traced much earlier, perhaps to the Triassic, using a technique called ghost lineages.

A ghost lineage is an evolutionary lineage that has left no fossil record, but the presence of which is inferred from closely related clades. Let us look at the phylogenetic tree of basal birds, or avialans, from the Early Cretaceous of China, where four successive clades—avialans, pygostylians, enantiornithines, and ornithuromorphs (fig. 5.15)—are shown in the phylogeny from primitive to derived condition. Avialans are the most basal ones (they branch off first), which makes them the oldest. However, the other three clades, pygostylians, enantiornithines, and ornithuromorphs, all appeared in the Early Cretaceous. Their Jurassic record is entirely missing. From phylogeny, we can speculate that each of these clades might have originated much earlier. For example, the common ancestor of two derived sister taxa, enantiornithines and ornithuromorphs, possibly originated in the Late Jurassic (according to our phylogenetic hypothesis) but there are no fossils; similarly, the common ancestor of the sister taxa pygostylians and enantiornithines must have originated earlier, perhaps the Early Jurassic; and the common ancestor of two basal sister taxa such as avialans and pygostylians must have

lived even earlier, somewhere around the Late Triassic. The sudden bursts of overlapping clades of early birds in the Early Cretaceous reflect the preservational bias of the fossil record; the common ancestor of all basal birds similar to *Protoavis* must have existed in the Late Triassic time. Future discovery may fill these major gaps in the early radiation of birds during Late Triassic and Jurassic periods. Fossil evidence in time and space tells a similar story about the antiquity of the origin of birds. The appearance of all major clades of Mesozoic birds in the Early Cretaceous Jehol biota (about 125 million years ago), including avialans, pygostylians, enantiornithines, ornithuromorphs, and ornithurines, suggests that the origin of birds must be a very ancient event, occurring at least in the Late Triassic, if we project all the ghost lineages back in time (fig. 5.15).

Protoavis shows a strange mosaic of primitive and advanced features of avialans and more derived birds. Some unambiguous avialan features in *Protoavis* include: (1) an avidiapsid condition of the temporal configuration where the orbit is confluent with two temporal openings; (2) a streptostylic quadrate with an orbital process; (3) a semilunate carpal as a single crescentic bone as in *Confuciusornis* and modern embryonic birds covering the second metacarpal; (4) heterocoelous cervicals; (5) a furcula with a hypocleidium; (6) a separate and flexible scapulocoracoid joint; (7) a strut-like coracoid with an acrocoracoid process; (8) a sternum with a ventral keel; (9) a long preiliac process of the ilium; and (10) fusion of the ilium with the ischium to enclose the ilioischiadic fenestra and renal fossa. *Protoavis* is considerably more advanced than *Jeholornis*, which is now considered the basal member of avialans. Its antiquity and derived morphology indicates that *Protoavis* is more closely related to pygostylians than is *Jeholornis*. It evolved specializations beyond the point at which it could be precluded from being ancestral to all later avialans. The tentative phylogenetic position of *Protoavis* in the avialan tree is shown in figure 5.16.

There are at least two phylogenetic interpretations for *Protoavis*. Either it is an independent Triassic iteration of avialan morphology, an example of convergent evolution; or, if we accept its anatomical characters at face value, it is the oldest member of the avialans and increases the time range of this group by as much as 75 million years. Although a Triassic avialan may seem unlikely at first, accepting its characters at face value and eschewing the ad hoc hypothesis of convergence, the conclusion that *Protoavis* is an avialan appears inescapable from anatomical features. If correctly assigned to the avialans, *Protoavis* is the oldest member of the group and pushes back the origin of avialans to the very dawn of the dinosaurs. This makes the fossil record of avialans the most extensive range of any group of dinosaurs.

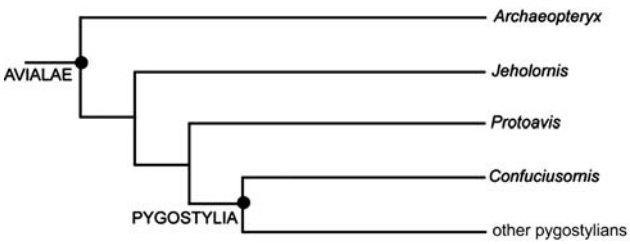


Figure 5.16. Cladogram showing the phylogenetic position of *Protoavis* among avialan birds.

Traditionally, birds are considered as the late evolution of theropods in the Mesozoic ecosystems (Ostrom 1976a, b, c). If we accept *Protoavis* as an early experiment in early bird evolution, most likely dinosaurs and birds evolved concurrently and sympatrically in two distinct ecospaces—early birds on trees and early dinosaurs on land. Time and again, birds and their theropod antecedents gave up flight during the Mesozoic and became terrestrial theropods, as Paul (2002) has suggested. In that case many lineages of theropods, especially the maniraptorans, might represent the flightless variants of birds throughout the Mesozoic. This may explain why maniraptorans are more bird-like with an encephalized skull, longer arms, contour feathers, and a crouching stance because they might have evolved from their flying ancestors as Paul has forcefully argued. Heterochrony and reversals might have complicated the ancestor-descendant relationships between theropods and birds and their phylogeny because avialans are recognized mostly by their flight-related attributes in their postcranial skeletons. In contrast, skull characters suggest the avialan affinity of *Protoavis*, which evolved independently of flight and thus are more reliable for diagnosis.

6 Basal Avialans: The Long-Tailed Birds

The trees belong to birds; no one transgresses these commands of this god Savitr.

Rig-Veda, ca. 1500 BC

Cretaceous Aviary

Birds originated during the Late Triassic period along with dinosaurs, about 225 million years ago. The emergence of birds was followed by a long period of stasis, or a phylogenetic fuse stage, when few species are recorded in the Late Jurassic time. The explosive evolution of birds took place in the Early Cretaceous when they expanded to many lineages with refinement of flight and a wide range of ecological adaptations. In the previous two chapters I discussed two long-tailed controversial basal birds—*Protoavis* from the Late Triassic of Texas and *Archaeopteryx* from the Late Jurassic of Germany. The controversy highlights how hard it is to distinguish basal birds from their immediate feathered paravian ancestors, which also acquired some degree of flying ability. Flight or feathers can no longer be used as defining characters of birds. In transitional forms, it is difficult to draw the line between nonavian paravians and early avialans, where the taxonomic boundary is blurred and diffuse.

Our current understanding of the origins and early evolution of birds has been strongly influenced by remarkable skeletons of basal avialans discovered during the past two decades from the Early Cretaceous Jehol Group as well as their immediate paravian relatives from the Middle-Late Jurassic Tiaojishan Formation of northeastern China. The Cretaceous period (about 144–65 million years ago) marks the first global radiation of birds. During this time, Laurasia and Gondwana fragmented; shallow seas invaded North America and Europe. Dinosaurs became endemic because of the isolation of continents and appeared more varied and diversified. Forests thinned but the landscape grew prettier and more colorful with the appearance of flowers. Flying creatures, ranging from the giant pterodactyls to modest-sized birds, were diversifying fast. Sea monsters such as plesiosaurs and mosasaurs dominated the shallow seas where food was abundant.

During the Early Cretaceous, China was a mosaic of small continental fragments, such as the North and South China Blocks and Tarim Block, separated by shallow seas (fig. 1.1). In these strange and isolated island continental assemblies, the avialan biota was evolving with extraordinary diversity and in a rapid pace in northeastern China. The forests and lakes of Liaoning were filled with exotic life, teeming with Cretaceous

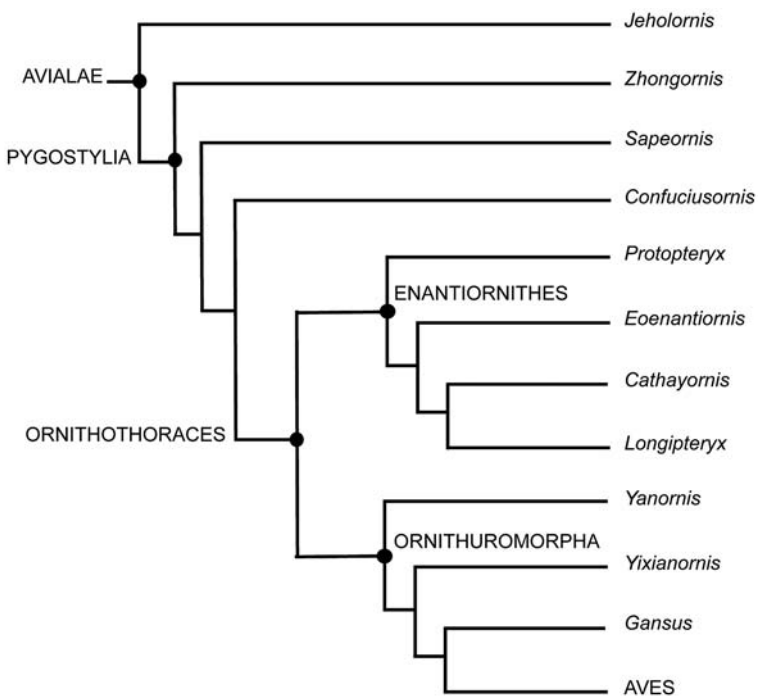


Figure 6.1. Cladogram depicting the phylogenetic relationships of selected taxa of Jehol birds from the Early Cretaceous of China.

birds and their relatives. The Jehol biota is a snapshot of evolutionary bursts, which were beautifully preserved in the Lagerstätten deposits. The unusually tranquil landscape of Jehol, as well as its flora and fauna, were under constant threat from recurrent volcanic episodes, which produced spewing ashes and deadly pollution that periodically led to catastrophic mass mortality; the entombed dead bodies of exotic flora and fauna were transported and deposited at the undisturbed bottom of lakes for posterity. In this life and death drama, the early avialan birds coexisted with their ancestors and descendants around the Jehol forests, which were punctuated by large lakes (fig. 1.2).

Evolution on a large scale unfolds, like much of human history, as a succession of dynasties. Long-tailed basal avialans, short-tailed pygostylians, the acrobatic enantiornithines, and progenitors of modern birds such as ornithuromorphs represent four such successive clades of Mesozoic birds, all present in the Jehol biota. They provide a rare window on the surprising and exotic diversity and evolution of Early Cretaceous birds in a single geographic locality and ecosystem. Thousands of specimens of these early birds were preserved in exquisite detail, as if the whole Mesozoic avian evolution was frozen in time in the finely deposited ash layers of the lakebeds of Liaoning. Currently, the Jehol biota comprises thirty-five genera and forty species of birds, which constitute approximately one-third of the known Mesozoic avian species globally, and radiated in four evolutionary pulses (Zhou 2008). These four successive clades of avialan radiation are beautifully documented in the ash beds of Liaoning along with their putative ancestors (fig. 6.1).

The first phase of radiation represents the basal avialans such as *Jeholornis* and their antecedents such as oviraptorosaurs, scansoriopterygids, deinonychosaurs, and tetrapterygids. The second phase of radiation includes the pygostylians such as *Zhongornis*, *Sapeornis* and *Confuciusornis* with the reduction of the bony tail and subsequent refinement of flight. The third phase of radiation consists of a wide range of enantiornithine birds with more acrobatic skill, such as *Protopteryx*, *Eoenantiornis*, *Cathayornis*, and *Longipteryx*. The fourth phase includes derived ornithuromorphs such as *Yixianornis* and *Yanornis* that led to the emergence of modern birds. The com-

mon ancestor of these two diverging clades—enantiornithines and ornithuromorphs—can be traced back to Ornithothoraces (Chiappe and Calvo 1994).

Many basal avialans retained primitive characteristics, such as a long bony tail, clawed wings, and teeth, but some of these features were lost with refinement of flight. Most of the Jehol birds are recognized as arboreal forms, representing the first major radiation in avialan evolutionary history. Jehol was a lost world with sounds and colors of feathered animals in the backdrop of a deep green tropical forest, often punctuated by first flowers, now gone and buried by the stone and clay of a past age. The Jehol fossils have greatly expanded our knowledge of the diversity and paleobiology of early birds, their flight and feathers, their food and habitat, their sex and behavior, their size and color, and their life and death (Zhang et al. 2008).

In this chapter I discuss the beginning of this sudden explosion of Cretaceous aviary as documented in China, emphasizing the significance of basal avialans in the radiation of birds. I have used the clade Avialae, first proposed by Gauthier (1986) and modified by Gauthier and de Queiroz (2001) and Xu et al. (2011). Avialae includes long-tailed birds such as *Archaeopteryx*, *Jeholornis*, and *Protoavis* and all pygostylian birds. Following Gauthier (1986), I have restricted the term "Aves" to the crown clade of birds (see chapter 11). I admit that the systematic position and composition of Avialae are in a state of flux. Future discovery of additional feathered paravians and their systematic analyses may settle the relationships and composition of Avialae.

The basal avialans refer to the group of early birds that retained a long bony tail (as opposed to a short bony tail) comprising typically more than twenty vertebrae that does not end in a pygostyle (O'Connor et al. 2011). The avialans show the following synapomorphies: the nostril moved back to lie partially above the antorbital fenestra, a prominent acromion process on the scapula, quill knobs on the ulna for flight feathers, a pointed and posterior process on the ilium, a reversed hallux, a procoelous synsacrum, the shaft of the ulna considerably thicker than that of the radius, a fibula that does not reach the proximal tarsus, and a tubercle on the dorsal face of metatarsal III.

As discussed earlier (see chapters 3 and 4), deinonychosaurs such as dromaeosaurs and troodontids are regarded as a sister group of Averaptora (Agnolin and Novas 2013). Among averaptorans, small four-winged tetrapterygids such as *Xiaotingia* and *Anchiornis* are so similar to *Archaeopteryx* that they are regarded as the close sister group of Avialae (fig. 4.6). Averaptora in my classification includes two clades: Tetrapterygidae and Avialae.

Jeholornis: An Archetypal Avialan

Unlike *Archaeopteryx*, *Jeholornis prima* represents an example of an unequivocal basal avialan in its body plan and anatomy. *Jeholornis* has been repeatedly found in the phylogenetic analyses to be the most primitive bird (Xu et al. 2011; Turner et al. 2012; Godefroit et al. 2013a, 2013b). Elongate grasping forelimbs and a long balancing tail characterize the skeleton of *Jeholornis*. Although the status of *Archaeopteryx* is uncertain right now, perhaps *Jeholornis* will become a similar iconic symbol of evolution, a new crown prince Urvogel for understanding early bird anatomy and the origin of flight.

Anatomy of *Jeholornis*

Currently, two valid species of *Jeholornis* are recognized: *Jeholornis prima* (Zhou and Zhang 2002) and *Jeholornis palmapensis* (O'Connor et al. 2011). The description that follows is a composite account of two species. The discovery of the first long bony-tailed, archaic bird from the Early Cretaceous Jiufotang Formation in the Hebei Formation of China, *Jeholornis prima* (= *Shenzhouraptor sinoensis*), has presented an interesting mosaic of primitive and advanced characters (Zhou and Zhang 2002, 2003). The skeletal architecture of *Jeholornis* differs significantly from that of *Archaeopteryx*. *Jeholornis* is a large bird, about the size of a turkey, with a length of up to 80 centimeters. The skull is fairly short and high relative to its length with an abbreviated snout similar to that of other primitive maniraptorans such as *Epidexipteryx*, *Caudipteryx*, and *Incisivosaurus*. *Jeholornis prima* lacked teeth in the upper jaw, and there are only three small teeth at the tip of the

dentary. The teeth are blunt and peg-like with no serrations. In contrast, *Jeholornis palmapensis* has several teeth in the middle of its maxilla (O'Connor et al. 2011). The external naris is oval and high relative to its length. The premaxilla is short and deep with a steep rostral margin. The maxilla is reduced and contains a large antorbital fenestra. Behind the fenestra, the lacrimal is T-shaped with two elongated pneumatic fossae and might have had a sliding contact with a slender jugal bar. The quadrate appears to be single headed with a synovial otic joint. The frontals expand caudally to form the orbital margin and contact the parietals, which are long, rounded, and oval-shaped, constituting the major part of the braincase roof, which appears to be inflated. The temporal configuration is modified from the diapsid condition of oviraptorosaurs where the squamosal-quadratojugal bar is lost in front of the quadrate and the contact of the postorbital and jugal bar is breached, making the quadrate streptostylic. It appears that *Jeholornis* had achieved some form of primitive kinesis, which culminates in modern birds (see chapter 15). The mandibles are robust with a downturned beak and a fused symphysis as seen in some oviraptorosaurs (fig. 6.2A).

The most exiting implication of the discovery of the *Jeholornis* skeleton is the preservation of seeds in the stomach, suggesting its seed-eating habit (granivory) (Zhou and Zhang 2002). The gradual reduction of teeth with the appearance of a beak-like structure in oviraptorosaurs and early birds have been implicated for herbivorous adaptation (Zanno and Makovicky 2011), but the skeleton of *Jeholornis* provides the first direct evidence for seed adaptation in early birds. There are about fifty ingested and intact seeds in the anterior stomach region of *Jeholornis* (see chapter 15). The abdomen was protected ventrally by the long, slender, and rod-like gastralia. It appears that herbivorous adaptation played a vital role in the early evolution of birds and their immediate ancestors.

The neck is short and the trunk is long in *Jeholornis*. There are about ten cervical vertebrae, which are robust and weakly elongate, followed by twelve dorsals, which are somewhat short, deep, and spool-like, often displaying pneumatic openings. Both prezygapophyses and post-

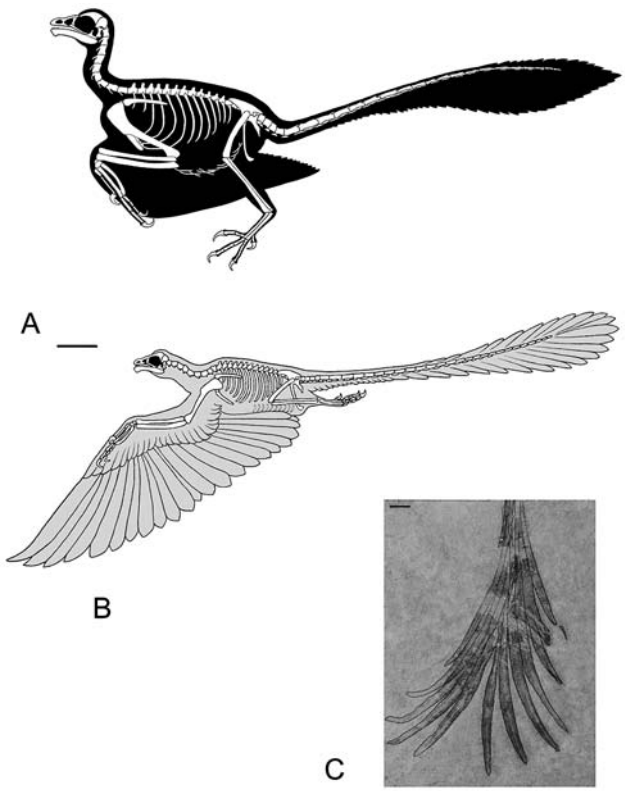


Figure 6.2. *Jeholornis* is one of the most primitive birds known in cladistic terms and may displace *Archaeopteryx* from the center stage in avialan evolution to become the new Urvogel. A, skeletal reconstruction of *Jeholornis prima*, a turkey-sized bird from the Early Cretaceous of China (modified from Zhou 2004). B, *Jeholornis* in flying posture; C, *Jeholornis palmapenis* had overlapping tail feathers resembling a fan-like palm frond at its end, which could function as a lifting surface and for sexual display.

zygapophyses are long and extend beyond the faces of the centra. The synsacrum is entirely covered by the pelvis but contains six fused sacrals. The last sacral has an expanded transverse process at the distal end and articulates with the first caudal. *Jeholornis* has a long bony tail, longer than the hindlimb, consisting of about twenty-seven caudal vertebrae, several more segments than *Archaeopteryx*. The caudal centra are narrow and elongate but gradually taper and shorten in the posterior direction. The anterior caudals are short relative to the middle and distal caudals and possess extensive elongate prezygapophyses and postzygapophyses for firm articulation. The middle and distal caudal series has elongated prezygapophyses and chevrons, resembling those in some dromaeosaurs and mak-

ing a stiff tail, which was possibly used as a prop during climbing trees (Chatterjee 1997).

Compared with *Archaeopteryx*, *Jeholornis* shows some advancement in the flight apparatus (fig. 6.2B). The shoulder girdle articulation of *Jeholornis* is mobile; the coracoid is elongate and strut-like, containing a supracoracoid foramen; the scapula is curved and tapered distally as in ornithurine birds. The glenoid faces dorsolaterally, which would have allowed both upstroke and downstroke of the wings. The furcula is robust and boomerang-shaped; the wide and short sternum is ossified with a lateral trabecula pierced by a fenestra.

The forelimb is proportionately longer than the hindlimb, indicating that the long wings were specialized for flying. The humerus has a large pectoral crest with a subdued ventral tubercle; the ulna is longer than the humerus; the carpometacarpus is fused proximally with a bowed metacarpal III (presumably one on each side), and it has a shortened and more robust digit 2, more suitable for attachment of flight feathers; the manus is short, as long as the humerus and radius, and bears powerful claws. The phalangeal formula is 2-3-4-x-x.

The pelvis has a build similar to that of *Archaeopteryx*; the ilium has a large, expanded preacetabular process and a stout pubic peduncle, the ischium is much shorter than the footed pubis, and three bones are unfused. The pubis is slightly retroverted from the vertical position. However, the dorsal process of the ischium is much more pronounced as in *Sapeornis*, *Confuciusornis*, and enantiornithines.

The femur is straight and robust, about 75% of the length of the tibiotarsus, indicating that *Jeholornis* was not a cursorial animal. Distally, the femur has a deep and narrow popliteal fossa in the caudal aspect, and the ectepicondylar tubercle is separated from the lateral condyle by a fibular groove. Proximally, the tibia lacks the cnemial crest; distally, the astragalus and calcaneum are not fully fused with the tibia to dorm the tibiotarsus; the astragalus has a tall ascending process in front of the tibia; the calcaneum is highly reduced. The fibula is slim and tapers distally about two-thirds the length of the tibiotarsus. The tarsometatarsus is fused at the proximal end. The fifth metatarsal is present as a splint as in *Archaeopteryx*, *Confuciusornis*, and *Sapeornis*. The hallux is reversed, and the claws in the foot are large and highly recurved for perching. The phalangeal formula is 2-3-4-5-0. The combination of derived pectoral girdles and forelimbs with very primitive hindlimbs and tails indicates the mosaic pattern of characters in the early evolution of birds.

Feathers are lacking in the holotype but are present in other specimens of *Jeholornis* (= *Shenzhouraptor*) (Ji et al. 2002a). The flight feathers in remiges are long and asymmetrical, longer than the forearm and hand combined. The tails of several specimens, especially in an allied species of *Jeholornis palmapensis*, show a fan of feathers like a palm frond that radiates from the twentieth caudal vertebra to the tip (O'Connor et al. 2011). A total of eleven feathers are preserved; six retrices are attached to the dorsal side, and five to the ventral side. Each feather is narrow with symmetrical vanes (fig. 6.2C). The feathers on either side of the bony tail are curved so that the cranial surface is concave and the caudal surface is convex. The function of the tail feathers is not fully understood but the tail could be used as a lifting surface, for pitch control during flight, or for sexual display to attract a mate.

The long-tailed *Jeholornis* can play a crucial role in understanding the evolution of short-tailed pygostylian birds such as *Zhongornis*, *Sapeornis*, and *Confuciusornis*. The flight apparatus of *Jeholornis* resembles that of *Confuciusornis* in form and function, with the forelimbs longer than the hindlimbs and short robust hands (Zhou and Zhang 2003). With the retention of the long bony tail supporting fan-shaped feathers, *Jeholornis* had a stable gliding flight. With the loss of the bony tail, the pygostylians probably became unstable but more acrobatic (see chapter 12).

Paleoecology of *Jeholornis*

The forests of various gymnosperms dominated the landscapes of Jehol environments and provided important cover and resting places for a variety of birds. In the lakes, the earliest angiosperms similar to lilies, such as *Archefructus*, thrived. Arboreal forms were dominant in the Jehol avialan assemblage, indicating that they may represent the most primitive ecological types in avialan history

(Zhou 2008). *Jeholornis* was probably an arboreal bird as is evident from the reversed hallux, large and recurved claws, and perching feet (Zhou and Zhang 2003). However, the toes' proportions are not characteristic of more advanced perching birds with distinctively longer penultimate phalanges. Apparently, *Jeholornis* did not have the sophisticated grasping and perching capacity of many modern perching birds. Most likely, *Jeholornis* spent most of its time in trees, feeding on seeds and avoiding predators. Its powerfully clawed hand, as long as the humerus, indicates its climbing ability. This primitive bird used its recurved claws and stiff tail for climbing vertical trunks. One of the enigmatic plant seeds was *Caprolithus*, relished by *Jeholornis*, as indicated by its stomach contents. These seeds are rounded, each about 8 to 10 millimeters in width of uncertain affinities. The seed-eating habit is reflected in the morphological features of the jaws of *Jeholornis*, where most of teeth were lost with the development of the beak.

Like *Archaeopteryx*, *Jeholornis* was probably a glider with a long bony tail and could launch from a perch. The weak hindlimbs and poor flapping ability suggests that *Jeholornis* could not take off from the ground. However, the skeletal features of the shoulders and wings of *Jeholornis* show substantial improvement in flight performance compared to those of *Archaeopteryx*. The elongated, strut-like coracoid, the laterally facing glenoid, the enlarged wing areas, the strengthening of the wrist, and the ossified sternum of *Jeholornis* suggest that this primitive bird was capable of rudimentary flapping flight, especially during takeoff and landing (see chapter 12). The wing proportion is also improved from the *Archaeopteryx* condition, where the ulna is longer than the humerus and the hand is relatively shorter. Pneumaticity is present in the thoracic vertebrae and sternum; the latter may indicate the presence of the interclavicular sac in *Jeholornis*, perhaps hinting at the beginning of an avian-like breathing mechanism. However, the presence of gastralia suggests that reptilian breathing system was still in place. The robust wings, strong shoulder girdle, and robust furcula and ossified sternum suggest that flight muscles in *Jeholornis* were moderately developed. However, the sternum had not developed any keel for the origin of enlarged flight muscles. The fan-shaped, overlapping retrices at the distal end of the tail, as seen in *Jeholornis palmapensis*, were probably used for lift and maneuvering as well as for courtship display. In modern birds tail fanning is perfected with the development of a pygostyle and rectrical bulbs, which are special adipose tissue structures lying on either side of the pygostyle that control the spreading of tail feathers from a closed resting condition. These fan-shaped tail feathers play an important role in generating lift and manipulating the flight surface (Gatesy and Dial 1996). In contrast, the tail feathers in *Archaeopteryx* were frond-shaped and had a limited range of lift surfaces. The evolution of the fan-shaped tail in *Jeholornis* improves stability and lift. Unlike modern birds, the basal avialans could not control the opening and closing of tail feathers, as they lacked a pygostyle and rectrical bulbs. These tail feathers were permanently in an open position; they could function as a lifting surface and could control pitch. However, the primary function of these elaborate and radiating tail feathers was possibly associated with signaling and sexual selection, as seen in modern birds. We see the beginning of a fan-shaped tail in *Jeholornis* that culminates in pygostylians. In addition to a fan-shaped tail, the fused synsacrum is enlarged, incorporating six vertebrae that provided further strength to the pelvis, a biomechanical reinforcement that became particularly important during landing.

Several other long-tailed birds very similar to *Jeholornis* have been reported from the Jehol Group, such as *Shenzhouraptor sinensis* (Ji et al. 2002a) and *Jixiangornis orientalis* (Ji et al. 2002b). Both taxa are now considered junior synonyms of *Jeholornis prima* on the basis of similar diagnostic features (Zhou and Zhang 2007; Wang et al. 2013). Another long-tailed controversial bird is *Dalianraptor cuhe*, which can be distinguished from *Jeholornis* on the basis of shorter forelimbs and flightless adaptation (Gao and Liu 2005). More recently, it has been suspected that the *Dalianraptor* specimen may have been forged for the fossil trade, representing a composite skeleton of *Jeholornis* with the wings replaced by the shorter forelimbs of a flightless theropod.

Zheng et al. (2013) reported reproductive follicles inside the body of an unusually preserved fossil of *Jeholor-*

nis in the position of the ovary. Like modern birds, the right ovary was probably lost in *Jeholornis* to reduce body weight in response to flight. Thus *Jeholronis* provides a wealth of information about the bauplan and lifestyle of early avialans: monoplane gliding ability (see chapter 12), feeding habit (see chapter 15), and reproductive strategy (chapter 13). Unlike *Archaeopteryx*, its phylogenetic position is secure among early avialans. As such, *Jeholornis* appears to be the ideal candidate for crowning a new Urvogel.

7 Pygostylia: The Short-Tailed Birds

The capacity to significantly alter lift and manipulate the flight surface without distortion may have been two factors favoring tail shortening and pygostyle development during avialan evolution.

S. M. Gatesy and K. P. Dial, *From Frond to Fan*, 1996

The Beginnings of Short-Tailed Birds

Moving up from *Jeholornis* on the cladogram of early birds, we come to the node Pygostylia, a group of birds that includes various Chinese taxa such as *Zhongornis*, *Sapeornis*, and *Confuciusornis*, as well as all other birds with an abbreviated bony tail where the distal-most tail vertebrae became fused into a single element called the pygostyle that supports the rectrices, or tail feathers. In basal avialans, the long bony tail was coupled with wings for balance and stability during gliding flight and was used for pitch control. A well-designed tail is one of the most effective stabilizers that give a flier passive stability. With the loss of long bony tail, which allowed tight aerial turning, the early pygostylians became unstable but more maneuverable in flight. The loss of a tail was such an important improvement in the evolution of avian flight that I named a new clade Pygostylia for these groups of birds to separate them from the primitive long-tailed avialans (Chatterjee 1997). Chiappe (2002) formally defined Pygostylia as the common ancestor of Confuciusornithidae and Aves plus all their descendants on the basis of following derived characters: absence of the hyposphene-hypantrum accessory articulation in the thoracic vertebrae, a pygostyle, a backwardly turned pubis at an angle of 45° to 65° below the vertebral column, and a wide and bulbous medial condyle of the tibiotarsus at the distal end.

Zhongornis, a transitional bird from the Early Cretaceous of China, provides an important link in the transition between avialans and pygostylians in tail anatomy; it has only thirteen caudal vertebrae (compared to twenty-seven in *Jeholornis*) but it lacks a true pygostyle. In *Sapeornis* and *Confuciusornis* a rod-like pygostyle supports tail feathers and musculature. In this discussion, *Zhongornis* is considered a basal member of the pygostylian radiation.

The loss of a tail occurred in all three lineages of flying vertebrates—birds, bats, and pterosaurs—with refinement of flight. In the avialan lineage, with an abbreviated tail, the pygostylians became more acrobatic and maneuverable than early avialans, but less stable; instability was probably compensated by neural control that might be reflected

by the enlargement of the brain and a specialized nervous system required for active stabilizing (Maynard-Smith 1952). As birds evolved, their nervous system acquired the sophistication and reflexes needed for improvement in flight performance. Evolution has clearly favored maneuverability at the expense of stability. Flying animals are inherently unstable. One of the simplest ways to achieve instability is to lose the bony tail, which is an effective stabilizing device (Alexander 2002). We see the beginning of this tail reduction in *Zhongornis*. Instability and maneuverability in pygostylians gave them an advantage in developing maneuvering flight and turning sharply in dense environments such as forests. Maneuvering flight precludes the use of a passive stabilizing mechanism but is aided by a specialized nervous system.

Modern birds have short, stumpy tails equipped with a fan of feathers. They use their tails primarily to adjust drag at slow speeds and during sharp turns, but not for stabilizing. Thus the evolutionary trend in birds is to start with some passive stability with a long balancing tail, as seen in *Jeholornis*, followed by less stability and a more maneuverable design of wings beginning with the pygostylians. They could make aerial turns by banking their wings, aided by their short tails. Thus the development of a pygostyle is a critical step in the evolution of flight performance with decreasing stability and increasing soaring capability.

It has been suggested that the pygostyle could have coevolved with the development of the rectrical bulb, a mass of muscle and fat that surrounds the pygostyle and controls the opening and closing of tail feathers. Most likely, tail fanning as seen in modern birds did not evolve in basal pygostylians but in more derived clades such as ornithurine birds with more refinement of flapping flight as reflected by their keeled sternums and powerful wing apparatus. In the basal pygostylian lineage, the pygostyle is rod-shaped, but in modern birds the pygostyle is a flat, plowshare-shaped bone that supports the rectrical bulb for tail fanning—spreading tail feathers from a closed resting condition to extension for altering lift and steering and manipulating flight (Gatesy and Dial 1996). Fanning and controlling of tail feathers was not possible in basal pygostylians with a rod-shaped pygostyle. The tail feathers of basal pygostylians were static and were primarily used for sexual display and additional lifting surface. The controlling mechanism of tail feathers first appeared in ornithurine birds as reflected by their plowshare-shaped pygostyle (Clarke et al. 2006).

Gao et al. (2008) put *Zhongornis* as the sister taxon to all birds with a pygostyle. Here I classify *Zhongornis* as a member of the basal pygostylians because of its abbreviated tail. Moreover, a fused pygostyle might occur in an adult individual of *Zhongornis*. In any case, *Zhongornis* plays a critical role in the early evolution of flight associated with decreasing stability with the loss of the tail and increasing maneuverability. A simple cladogram of pygostylian birds is shown in figure 7.1.

Zhongornis: The Beginning of Pygostylians

Zhongornis (meaning "intermediate bird") from the Early Cretaceous Yixian Formation of China is known from a single species, *Zhongornis haoae* (Gao et al. 2008). It is a transitional bird bridging the morphological gap of tail structure between the long-tailed *Jeholornis* and the short-tailed pygostylians ending in a fused pygostyle. *Zhongornis* shows evidence of a truncated bony tail containing thirteen caudals, about half the number of *Jeholornis*, but the tail lacks a pygostyle (fig. 7.2). So far, *Zhongornis* is the only bird known to possess a short tail with a reduced number of vertebrate, yet lacks the true pygostyle present in other short-tailed birds, a transitional character expected in the beginning of a clade. In *Zhongornis*, the four distal-most caudals appear to form a continuous lateral flange, which gives the appearance of an incipient pygostyle. In contrast, *Sapeornis* and *Confuciusornis* had ten unfused caudal segments, followed by a long and fused pygostyle with a prominent axial keel along the entire length (fig. 7.3).

The development of pygostyle played a key role in the Cretaceous diversification of birds with refinement of flight. *Zhongornis* provides an important clue to the sequence of acquisition of a pygostyle in pygostylians: decrease in relative tail length and number of caudal vertebrae, followed by distal fusion of the caudals into a

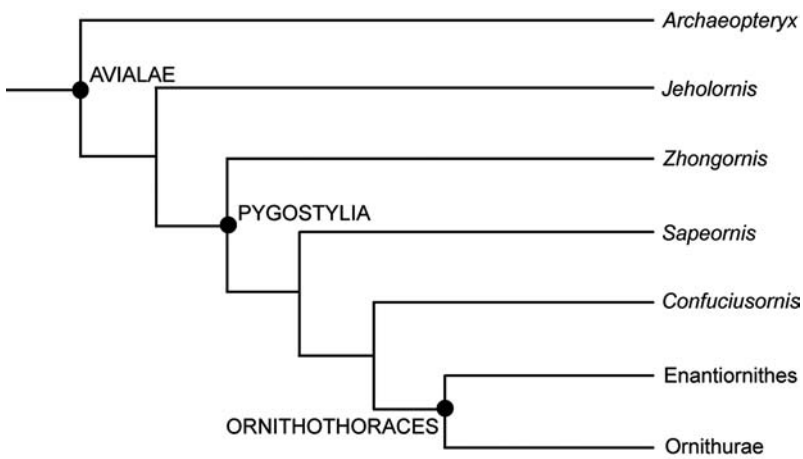


Figure 7.1. Cladogram showing the relationships of short-tailed pygostylians.

rod-like pygostyle. Later in this evolutionary sequence, the rod-like pygostyle was morphed into a plowshare-shaped pygostyle that would accommodate a rectrical bulb. The lack of ossification of a pygostyle in *Zhongornis* might reflect the juvenile nature of the only specimen. Other elements, such as the carpometacarpus, the synsacrum, the tibiotarsus, and the tarsometatarsus, are also unfused.

Zhongornis shows several derived features relative to *Jeholornis* but some of the features are not fully expressed because of the juvenile nature of the specimen (fig. 7.2B). The skull is somewhat crushed dorsoventrally and is difficult to interpret, but shows edentulous jaws, a highly inflated braincase, a large orbit, and a short beak as in *Confuciusornis*. The postorbital bar is complete, showing the contact between the postorbital and jugal bone. The quadrate has a broad orbital process. The neck is short, containing at least nine cervicals, followed by thirteen to fourteen thoracic vertebrae with ribs attached that lack uncinate processes. There may be six or seven sacrals and thirteen caudals. The coracoid is strut-like and expanded proximally as in volant birds. The stout furcula is boomerang-shaped. The humerus is longer than the ulna. Unlike in enantiornithine birds, the deltopectoral crest of the humerus lacks a foramen. The manus is large and equipped with terminal claws; the largest manual claw is on digit 1, with unguals 2 and 3 subequal; the phalangeal formula is 2-3-3-x-x, showing the avian trend toward phalangeal reduction. The pelvis is poorly preserved; the ilium is shorter than the femur. The tibia is straight and shows an astragalus and a calcaneum distally that are not fused to form a tibiotarsus. The fibula is reduced to a splint. The metatarsals are unfused, but there is a reversed hallux that is shorter than the other digits. Only faint traces of remiges are preserved in the right hand. The tail feathers show nonaerodynamic feather tufts (fig. 7.2A).

Sapeornis, the Largest Pygostylian in the Early Cretaceous

Sapeornis chaoyangensis from the Early Cretaceous Jiufotang Formation of China was a large, short-tailed primitive bird with a wingspan of nearly 1 meter (comparable to that of a gull) and may represent the largest bird from the Jehol biota. It was a basal pygostylian with a fused pygostyle and enormously elongated forearms. The genus was named in honor of the Society of Avian Paleontology and Evolution (SAPE) conference, which was held in Beijing in 2000 (Zhou and Zhang 2002). The skull of *Sapeornis* is relatively short with four conical, robust, and unserrated teeth in the premaxilla and a few teeth in the anterior part of the maxilla but the dentary is toothless. The lacrimal is long and tapering ventrally, separating the triangular antorbital fenestra from the large circular orbit,

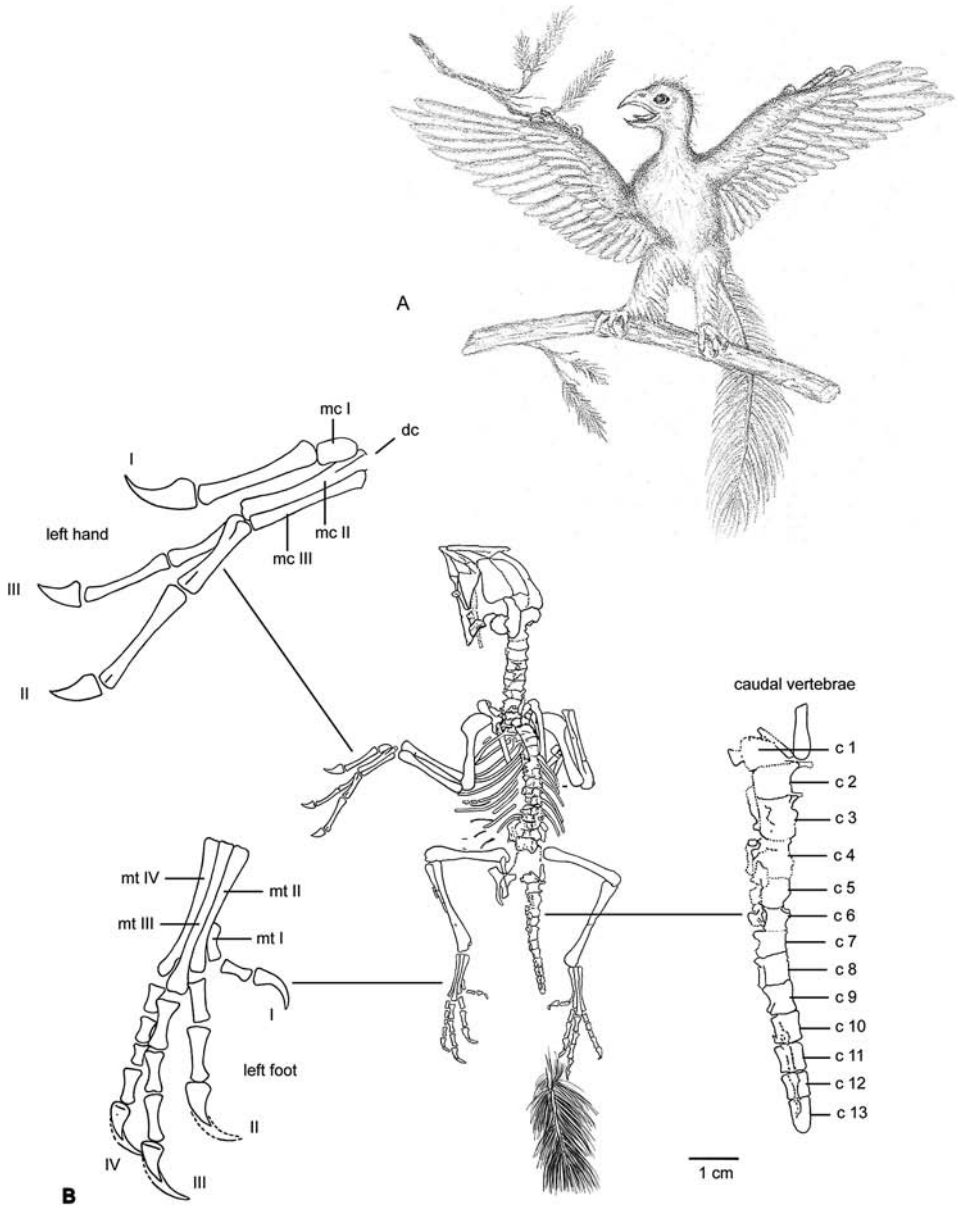


Figure 7.2. *Zhongornis haoae*, a basal member of the pygostylians from the Early Cretaceous of China. A, life restoration of *Zhongornis*. B, the dorsal aspect of the skeleton as preserved showing the critical anatomical features of a transitional bird bridging the morphological gap between long-tailed avialans and short-tailed pygostylians. *Zhongornis* shows the phalangeal reduction of hands with a phalangeal formula of 2-3-3-x-x and the abbreviation of the bony tail that contains only thirteen caudal vertebrae but lacks a true pygostyle. *Zhongornis* is the close sister taxon to all pygostylians (Gao et al. 2008).

but it lacks contact with the slender jugal bar. The frontal is expanded and the parietal is short and square-shaped. The temporal region of the skull shows little modification from the primitive diapsid condition; the upper temporal opening is intact, but the orbital and lower temporal arches are slightly modified. The postorbital-jugal bar appears to be breached, and the squamosal-quadratojugal bar in the front of the quadrate is highly reduced. The quadrate has a slender orbital process and is somewhat kinetic. The lower jaw is robust and toothless with a

mandibular symphysis and it lacks the mandibular fenestra (fig. 7.3A).

There are about ten cervical, thirteen thoracic, seven sacral, and seven free caudal vertebrae and a long, triangular pygostyle. The cervical vertebrae are elongate and heterocoelous, and thus exhibit a more derived condition from *Jeholornis*. The thoracic vertebrae are amphicoelous but lack true pleurocoels. The synsacrum is composed of seven fused vertebrae as in *Confuciusornis* with a deep conjoined spinal crest and flared transverse processes that become more robust caudally. The free caudals are short and small compared to the preceding sacrals. The pygostyle is long and triangular as in enatiornithine birds. The ribs are long and slender but lack uncinate processes; the gastralia comprise at least fifteen pairs of slender long bones in the abdominal region (fig. 7.3A).

The scapula and coracoid articulate at an acute angle as in other volant birds. The scapular shaft is nearly straight. tapers slightly toward the distal end, and it lacks a prominent acromion process proximally. The coracoid is primitive, broad and short, and trapezoidal, and contains a supracoracoid foramen. The glenoid facet of the coracoid lies ventral to the acrocoracoid process. The furcula is robust and Y-shaped with a moderately developed hypocleidium. The sternum is not present, probably unossified, indicating paedomorphism.

Sapeornis had long and powerful wings but retained small symmetrical metatarsal feathers as in primitive tetrapterygids such as *Pedopenna* and *Anchiornis* with an abbreviated biplane wing design (fig. 7.3B). The forelimb of *Sapeornis* is slim and extremely elongated, about 1.5 times the length of the hindlimb. The humerus is highly expanded proximally where the deltopectoral crest is large with a straight dorsal margin and is perforated by a large oval foramen of uncertain function. The proximal head is somewhat spherical but lacks the capital groove and pneumatic fossa. The bicipital crest is small and flat. Distally, the articular condyles are well developed and anteriorly placed; the dorsal condyle is subdued, but the ventral condyle is spherical and well pronounced. The ulna is slightly longer than the humerus; it is curved along the proximal shaft but becomes straight distally and lacks quill knobs. Proximally, the olecranon process is short and stout; the distal end is not much expanded and lacks a semilunate ridge for rolling against the ulnare. The radius is a straight, slimmer, and rod-like bone. The manus was as long as the ulna and was far more advanced than that of *Jeholornis*. The ulnare shows a well-developed V-shaped morphology as in modern birds. The radiale is as large as the ulnare and articulates proximally with the radius and distally with the carpometacarpus. The carpometacarpus is partially fused with the development of a

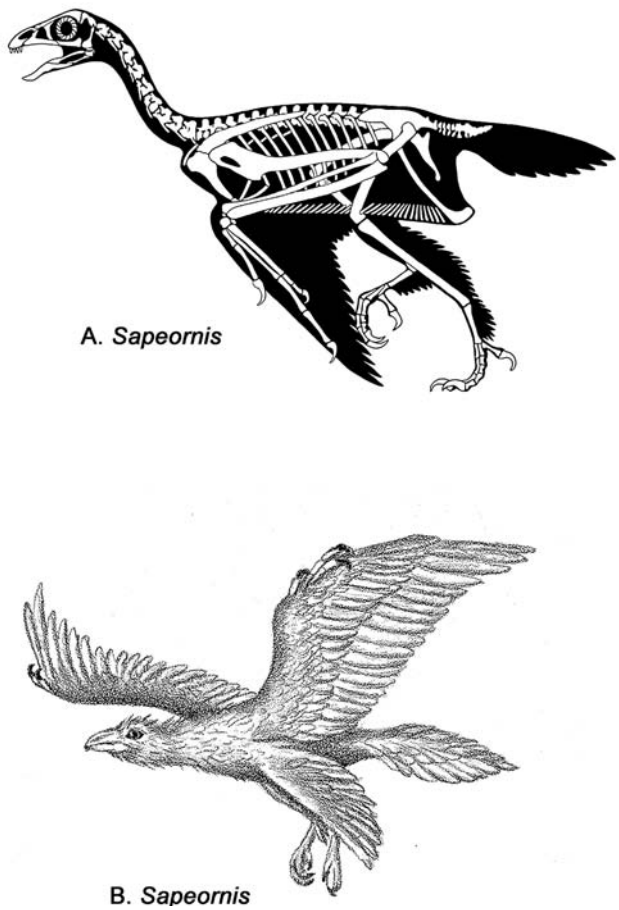


Figure 7.3. *Sapeornis chaoyangensis*, the largest early Cretaceous bird with a wingspan of about 1 meter, was a primitive member of the pygostylians. A, skeletal restoration of *Sapeornis*; the skull's modified temporal region permitted primitive kinesis (Zhou and Zhang 2003). B, gliding posture of *Sapeornis* showing retention of primitive small and symmetrical metatarsal feathers as seen in tetrapterygids such as *Pedopenna* and *Anchiornis*, but more reduced.

proximal trochlea and contains three fused metacarpals. Metacarpal I is short and straight; metacarpals II and III are highly elongate and of equal length, but the former is stouter than the latter. The third digit consists of a slender metacarpal and two small and slender digits. The phalangeal formula is 2-3-2, retaining terminal claws, but shows digital reduction.

The pelvis is primitively designed like that of basal avialans and three elements remained unfused. The ilium has a long preiliac process but a short postiliac process, and is not fused with the sacrum to form a synsacrum. The acetabulum is large and lacks the antitrochanter process; the pubic peduncle is robust and wider than the ischiadic peduncle. The pubis is long and slender with a distinct foot and is considerably retroverted. The pubic symphysis is extensive—about one-third the length of the pubis. The ischium is short and robust with a prominent strut-like dorsal process.

The hindlimb is relatively short compared to the forelimb as seen in enatiornithine birds. The femur is a stout and curved bone, with a spherical inturned head and a subdued greater trochanter at the proximal end. Distally, the femur is expanded into two condyles; there is a shallow intercondylar sulcus and the femur contains a prominent fibular groove. The bone is slightly shorter than the tibiotarsus. The tibiotarsus is short and lacks a prominent cnemial crest at the proximal end. Unlike the condition in *Jeholornis*, the tibia is fused with proximal tarsal bones at the distal end to form the bird-like tibiotarsus, where the two condyles are well developed. The fibula is extremely slender and rod-like and extends almost to the distal end of the tibiotarsus. The tarsometatarsus is also fused and is slightly constricted distally. Metatarsals II–IV are subequal in length, closely compressed proximally, but diverge distally; the fifth metatarsal is present as a splint in the proximal head; metatarsal I is short and J-shaped, and articulates distally with metatarsal II. The pedal digits are as long as the tibiotarsus with highly recurved claws for perching. The pes is anisodactyl, with a reversed digit 1; digits 2–4 are subequal in length. The phalangeal formula is 2-3-4-5-x.

Sapeornis includes two species: *S. chaoyangensis* and a smaller species *S. angustis*. In 2008, a new specimen related to *Sapeornis* was described as *Diadactylornis jii*. Recent analysis suggests that all other named sapeornithids are junior synonyms of *S. chaoyangensis* (Gao et al. 2012).

Confuciusornis, the Earliest Beaked Bird

Confuciusornis sanctus is one of the most abundant and best known of all Mesozoic birds with more than one thousand exquisite specimens in Chinese museums that provide critical information on anatomy, plumage, and inferred lifestyle (Hou et al. 1995, 1999; Chiappe et al. 1999; Martin et al. 1998). In one fossil site, forty skeletons of *Confuciusornis* were discovered in a single bedding plane of 100 square meters. Such a dense concentration of specimens suggests their highly social and gregarious lifestyle along the margin of a freshwater lake. Possibly the entire flock of birds was killed simultaneously by ash, heat, or poisonous gas from a volcanic eruption.

Confuciusornis is known from the Early Cretaceous Yixian and Jiufotang Formations of China and provides the earliest record of a toothless, beaked bird. Several species of *Confuciusornis* have been named in recent decades, but only two valid species are currently recognized: *C. sanctus* and *C. dui* (Hou et al. 1999). Another closely related smaller species, *Chanchengornis hengdaoziensis*, is known from a single specimen from the Yixian Formation (Chiappe 2007). Our discussion is mainly centered on *C. sanctus*.

The skull of *Confuciusornis* lacks teeth, but the impression of the horny rhamphotheca is preserved. The horny bill extends in front of the bony core with a long and pointed beak that curves upward. The subtriangular external naris, bounded by the premaxilla and the maxilla, has been shifted posteriorly from the bill's tip. At the skull roof, the conjoined premaxillae extend considerably backward to contact the frontals, thus displacing the nasals as in modern birds, but the prokinetic hinge was not developed. The frontals are inflated, showing the expansion of the cerebral lobes. In lateral aspect, the nasal process of the maxilla contains a small accessory fenestra as in some tetanurans; behind it, the antorbital fenestra is considerably reduced as a slit. The orbit is large, pro-

tected by a sclerotic ring. The temporal region retained an intact diapsid condition with a stout postorbital-jugal bar and a squamosal-quadratojugal bar, thus prohibiting streptostyly and cranial kinesis (Hou et al. 1999) (fig. 7.4A). Most likely, the redevelopment of intact diapsid arches and loss of kinesis in *Confuciusornis* may be the result of a reversal, possibly linked to a change in feeding habits (see chapter 15). The mandible is robust with a strong symphysis and contains a large external mandibular fenestra.

The neck is relatively short; the vertebrae show an incipient degree of heterocoely with deep pleurocoels. The thoracic vertebrae are amphicoelous. There are eight cervicals, thirteen thoracics, seven fused sacrals, seven free caudals, and a pygostyle. The uncinate processes are present in the thoracic ribs. The exact number of caudals involved in pygostyle formation is unknown because of intimate fusion, but the pygostyle may contain eight to ten elements. The pygostyle is triangular with central and transverse ridges. Ventrally it bears a prominent axial keel along its entire length.

The scapula and coracoid are fused into a rigid structure in nonavian fashion, where the two elements join at a right angle. The scapula is narrow and straight with a large acromion process; the coracoid is robust and strut-like and contains a large coracoid foramen, but it lacks the procoracoid and acrocoracoid processes. The glenoid faces sideways, instead of angled upward as in modern birds, indicating that the upstroke was feeble in *Confuciusornis*. The furcula is robust and boomerang-shaped but lacks the hypocleidium. The sternum is relatively long and flat without any keel, and the coracoid abuts directly against an oval facet on the anterior margin. As in basal avialans, *Confuciusornis* retained a full set of gastralia.

The forelimb bones retain primitive proportions as in *Archaeopteryx*—the hand is the longest segment, and the ulna is shorter than the radius. The humerus is short and robust with a flat or concave head and a large deltopectoral crest, which is pierced by a large oval foramen as in *Sapeornis*. Distally, the humerus is somewhat expanded with the development of two condyles on the cranial surface for articulation with the radius and ulna.

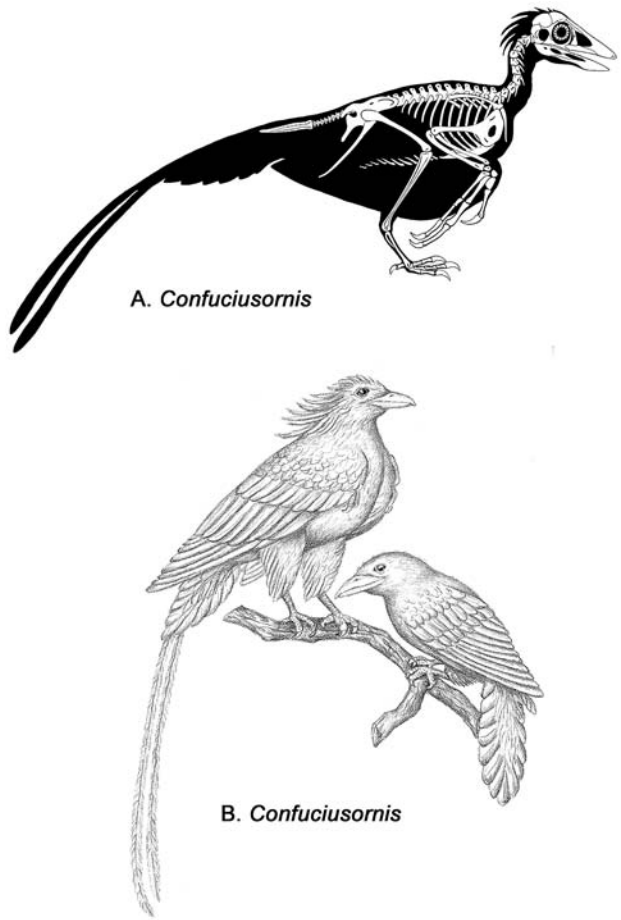


Figure 7.4. *Confuciusornis sanctus*, the earliest beaked bird from the Early Cretaceous of China. A, skeletal restoration of *Confuciusornis* depicting the rod-shaped pygostyle; the skull has a horny beak, toothless jaws, and an intact diapsid arch that would prohibit cranial kinesis (modified from Chatterjee 1997). B, life restoration of a pair of *Confuciusornis* showing the sexually dimorphic tail; the male sported two greatly elongated streamer-like tail feathers while the female's tail probably lacked them (modified from Zhang et al. 2008).

These two bones are essentially straight, but the ulna is somewhat bowed and it lacks any quill knobs. Distally, two proximal wrist bones, the radiale and ulnare, are well developed for articulation with the pulley-like trochlear surface of the carpometacarpus. The manus is equipped with sharp and recurved claws encased in enormous horny sheaths as in avialans to facilitate tree climbing. Metacarpal I is small and separate; metacarpals II and III are fused and long. The second metacarpal supporting

the primary feathers was strongly built; its finger carries a small and subdued claw. The phalangeal formula is 2-3-4-x-x (fig. 7.4A).

The pelvis is narrow and opisthopubic, connected to a sacrum formed by seven sacral vertebrae to form a synsacrum. The ilium has a long and broad preacetabular process but a short and narrow postorbital process. The acetabulum is completely open for the reception of the femur. The pubis is long and rod-like, retroverted without the development of any foot, and terminates distally at a symphysis. The ischium is relatively short and broad with a large dorsal process directed toward the ilium. The two ischia are not fused.

The femur is relatively straight with a spherical and inturned head, separated from the shaft by a neck. The proximal head contains a round capital fossa. The shaft is rounded in cross section. Distally, the femur is expanded with the development of articular condyles; there is a well-developed fibular trochlea, clearly separated from the tibiofibular crest. The tibiotarsus is straight and slightly longer than the femur. Distally, the astragalus and calcaneum appear to be completely fused to each other and to the tibia. The fibula is narrow and fits proximally with the fibular crest of the tibia. Distally it becomes narrow and rod-like and does not extend to the ankle. The tarsometatarsus is relatively short and fused proximally but not distally as in avialans and enantiornithine birds. Metatarsal I is attached distally to the lateral side of metatarsal II to form an anisodactyl foot. Metatarsal III is the longest in the series. A rudimentary fifth metatarsal is present. The terminal claws are highly recurved as in perching birds. The phalangeal formula is 2-3-4-5-x.

Paleoecology of Basal Pygostylians

Modern birds have no teeth. Seed-eating birds use their strong beaks to crack seed shells; they swallow the soft part of the seeds, or endosperms. Their digestive passageway is greatly expanded as a crop to hold large quantities of food in transit for softening seeds before passing them through a specialized stomach, or gizzard. Recent study suggests that *Sapeornis* may have had a modern seed-eating digestive system. The presence of gastroliths in *S. chaoyangensis* (Zhou and Zhang 2003) and the reduced teeth suggest that *Sapeornis* was probably an herbivore. Recent discovery of a crop in an articulated skeleton of *Sapeornis*, roughly in the same position as in modern birds, is densely packed with more than seventy small seeds, implying that crops might have developed in the early evolution of birds since the Early Cretaceous time (Zheng et al. 2011). Perhaps its incisor-like premaxillary teeth were used for stripping seeds from branches and the edentulous mandible and the maxilla were used for cracking seeds. The unusual preservation of stomach contents suggests that both *Jeholornis* and *Sapeornis* were seed-eaters. Moreover, these early birds probably played an important role as seed-dispersers that may have helped plants to colonize a wide range of habitats. There may be a correlation between a seed-eating habit (granivory) and the gradual loss of teeth in ancient birds.

Sapeornis was the largest known bird of its time and place (about 33 centimeters long and 5 kilograms in weight) with a wingspan of nearly 1 meter (comparable to that of a gull). The flight apparatus shows a mosaic of primitive and derived characters. Some skeletal features in *Sapeornis* point to substantial improvement in flight performance from the *Jeholornis* condition, including a furcula with a hypocleidium, an extremely elongated wing, a robust humerus with a distinctive head and large deltopectoral crest, a fused carpometacarpus with a well-developed carpal trochlea, reduced manual phalanges, and a pygostyle. Other features such as a short and primitive coracoid and an unossified sternum indicate that *Sapeornis* was not an active flapping flier. Feathers are preserved in exquisite details in a subadult specimen, where primaries and secondaries in the wings are long and asymmetric, indicating their aerodynamic function (Gao et al. 2012). However, they retained small symmetrical contour feathers in the hindlimbs including the metatarsus like those of *Pedopenna* and *Anchiornis*, indicating biplane wing configuration (see chapters 3 and 14). The retention of four primitive wings in *Sapeornis* like those of nonavialan maniraptorans as well as an unossified sternum must be an evolutionary reversal, an example of paedomorphism (fig. 7.3B). The reduction of leg feath-

ers and outright loss of pedal feathers occurred with the evolution of maneuverable flapping flight in ornithuromorph birds. *Sapeornis* had an opposable hallux, a long first pedal digit, and large and strongly recurved claws—all these features indicate its perching and arboreal habit. Because of its large wings, *Sapeornis* probably avoided dense forests and lived in open areas. Taking off from a perch would help *Sapeornis* to glide effortlessly in undulating fashion from tree to tree.

Confuciusornis was a crow-sized bird with a wingspan up to 0.7 meter and its body weight has been estimated as much as 1.5 kilograms. With its reversed hallux, strongly recurved claws, short tarsus, and elongated tail feathers, *Confuciusornis* was probably a perching bird and used its scansorial hands with large claws to climb tree trunks (Zhou et al. 1998). The loss of teeth and the appearance of a horny beak may indicate that these early birds may have swallowed their food and shifted the masticatory process mainly to their gizzards. Many *Confuciusornis* skeletons show beautiful impressions of contour feathers like those of modern birds, showing the details of vane structure including rachises, barbs, and barbules. There appears to be sexual dimorphism among *Confuciusornis* specimens, as reflected by tail feather impressions (Martin et al. 1998; Zhang et al. 2008). Male and female individuals were often found together preserved in one slab; presumably male birds sported a pair of long streamer-like tail feathers (longer than the entire length of the rest of the body) for sexual display, but the females lacked them (fig. 7.4B). A close relative of *Confuciusornis*, *Changchengornis*, also shows sexual dimorphism of feathers, short versus long tail feathers, as did several more advanced enantiornithine birds much like those of modern birds. Apparently, these early birds developed this complex social behavior of courtship displays. Sexual selection played a critical role in the early evolution of birds, even before the flight was perfected. *Confuciusornis* probably lived in flocks along the margin of a freshwater lake using its soft bill to catch fish and aquatic animals while swimming. Recent discovery of fish remains in stomach contents suggests that *Confuciusornis* reverted to a carnivorous diet like that of its ancestors.

Unlike *Sapeornis*, *Confuciusornis* lost the large pennaceous feathers in the legs and feet to become a monoplane flier, with the forelimbs as the sole lifting surface. Despite the development of a pygostyle, *Confuciusornis* was a poor flier as reflected by the primitive design of its flight apparatus. The scapulocoracoid becomes fused like in nonavian theropods, not flexible like in modern birds; its coracoid is short and lacks the supracoracoid pulley that allows uplift of the wing; the glenoid facet faces laterally rather than upward, suggesting that a normal upstroke would be difficult for *Confuciusornis*. The sternum is flat in *Confuciusornis*, suggesting that flight muscles were weak and subdued. In modern birds, the deep keel in the sternum houses the powerful flight muscles. Although the primary feathers are highly asymmetrical in *Confuciusornis* as in flying birds, these feathers have narrow vanes and the central rachis is too narrow and weak in cross section to withstand a compressive downstroke. The alula for controlling slow flight was not developed in *Confuciusornis*. The lateral position of the glenoid, absence of a supracoracoideus pulley, the flat sternum, and structurally weak flight feathers preclude vigorous flapping flight.

However, *Confuciusornis* had evolved long and narrow wings of high aspect ratio like those of gulls and their asymmetric flight feathers, suggesting that it was an excellent glider. It developed a propatagium, the lift-generating skin fold joining the shoulder and wrist. Because of underdeveloped flapping capability, *Confuciusornis* would not be able to take off from the ground. Moreover, the long tails in male individuals would interfere with a terrestrial lifestyle. However, *Confuciusornis* could launch from tree branches to pick up flight speed and glide in phugoid fashion from tree to tree in undulatory fashion without flapping its wings or land on lakes for foraging. The instability created by the loss of the bony tail was not an impediment for gliding flight but opened a new opportunity for *Confuciusornis* by developing maneuverable wings for aerial turns. Animal flight is not useful if a flying animal cannot maneuver or choose its own direction intentionally (Alexander 2002). *Confuciusornis* traded off maneuverability at the expense of stability. The development of a

pygostyle made *Confuciusornis* more maneuverable when circling in thermals during long-distance travel between its roost sites and feeding areas. To stay within a thermal, *Confuciusornis* was capable of turning in fairly tight circles as close as possible around the center of the thermal by banking its wings. Perhaps *Confuciusornis* became the first maneuverable soaring bird over the open areas of Jehol, relying on thermals where altitude was maintained or gained by rising air (fig. 7.3D). Flapping flight must have appeared within the enantiornithine radiation with the development of a powerful and sophisticated flight apparatus.

The systematic position of *Confuciusornis* in the phylogeny of birds is controversial. Some workers put *Confuciusornis* as a member of pygostylians; others classify it as a basal member of enatiornithine birds, the more sophisticated flying birds that will be discussed in the following chapter. However, because of lack of development of flapping flight, I prefer to classify *Confuciusornis* as a member of pygostylians but the closest relative of enantiornithine and ornithuromorph birds, grouped in a large clade of Ornithothoraces (fig. 7.1A).

The name Ornithothoraces means "bird thoraxes," referring to the modern, highly derived anatomy of the thorax and flight apparatus that gave these birds superior flight capability compared to that of basal pygostylians. The clade Ornithothoraces is composed of the most recent common ancestor of *Protopteryx* (a primitive enatiornithine bird) and ornithuromorph birds. I am splitting the discussion on ornithothoracine birds into two chapters, first describing an archaic lineage of enantiornithine birds that dominated the inland ecosystems of the Cretaceous and then more derived ornithuromorphs that would eventually give rise to modern birds.

8 Enantiornithes: Global Cretaceous Birds

The birds made dips and circular movements,
that were fluent and organized. As the huge swarm flew towards
their destination, one small speck of a bird left the pack and
flew in the opposite direction.

Benjamin Firsick, age 11, *The Opposite Direction*, Stone Soup, 2007

The First Pulse of Explosive Evolution

The Cretaceous period (about 144–65 million years ago) marks the first global radiation of birds. During this time, Laurasia and Gondwana fragmented; shallow seas invaded North America and Europe. Dinosaurs became endemic because of the isolation of continents and appeared more varied and diversified. Forests thinned but the landscape grew prettier and more colorful with the blooming of flowers in lands and lakes. Flying creatures, ranging from giant pterodactyls to modest-sized birds, were diversifying quickly. Marine reptiles, such as plesiosaurs and mosasaurs, dominated the shallow seas, where food was abundant.

Ornithothoraces is a clade that includes Enantiornithes and Ornithuromorpha, plus all their descendants (Chiappe and Calvo 1994). The name refers to a modern, highly derived anatomy of the thorax that gave the ornithothoracines flight capability superior to that of more primitive basal pygostylians. The anatomy includes a rigid thorax with elongated coracoids; a large, keeled sternum; and a modified glenoid of the shoulder joint for rapid wing strokes. Before the great radiation in the Cenozoic of modern birds (Aves), which evolved from ornithuromorphs, the flying Enantiornithes dominated the Mesozoic avifauna all over the world. In basal pygostylians we saw the abbreviation of the tail that made them inherently instable, perhaps to help them make quick aerial turns for circling in thermals or perching and landing in a tight arboreal habitat. Most likely, the abbreviated tail in concert with the wings was an aerodynamic breakthrough for enantiornithine birds and opened up a great diversity in Cretaceous ecosystems. In these birds, we see the further upgrading of the flight apparatus from their pygostylian ancestors that enabled them to flap their wings and made them more maneuverable and acrobatic for long-distance travel across the continents and oceans. Flapping flight allowed them to explore a wide range of environments and feeding styles.

Enantiornithines lived in the shadow of the great Cretaceous dinosaurs. Their fossils have been found in North America, South America, Europe, Asia, Madagascar, and

Australia at a time when Pangea had rifted and drifted apart considerably. Both the breakup of the supercontinent Pangea around 120 million years ago and the long-distance flight capabilities of Enantiornithes could be direct factors behind their diversification in the Cretaceous world. They had a modest beginning in the Early Cretaceous as represented by primitive toothed birds such as *Protopteryx* and *Eoenantiornis* from China but underwent an explosive evolution and expanded their range globally during most the Cretaceous with major improvement in their flight apparatus. But as befits their transitional status, they also retained some primitive characteristics not seen in modern birds in the skull, flight apparatus, pelvic girdle, and hindlimbs. Almost all enantiornithines retained teeth and clawed fingers on each wing. After their explosive evolution in the Cretaceous and their successful radiation, Enantiornithes died out suddenly at the terminal Cretaceous extinction along with nonavian dinosaurs and hesperornithine and ichthyornithine birds, leaving no descendants. They are essentially an extinct group of Cretaceous birds that experimented with flapping flight somewhat in a different style from that of modern birds.

Opposite Birds

In 1981, Cyril Walker described and identified a new clade of birds from the Late Cretaceous Lecho Formation of El Brete, in the Salta Province of Argentina, on the basis of isolated bird bones amassed by Jose Bonaparte. The bones were associated with a gigantic titanosaurid skeleton of *Saltasaurus*. Of the sixty or so bones found in El Brete, only a handful was in articulation. Walker noted a series of novel features in these isolated bird bones, including a reverse articular arrangement between the scapula and the coracoid, where the coracoid forms a peg to fit into the socket of the scapula. Moreover, a groove on the ventral surface of the scapula forms the most important part of the triosseal canal, the supracoracoideus pulley that elevates the wing. In neornithine birds, it is the dorsal end of the coracoid, the procoracoid process, which serves this role. On the basis of this reverse shoulder joint articulation, Walker attributed some of these disarticulated assemblages of bird bones to a new species, *Enantiornis leali*—a curious fossil bird so different and stunning in anatomy from other known birds that he erected a distinct lineage or subclass, Enantiornithes, meaning "opposite birds." Little did he realize that the Enantiornithes were soon to become the best-known and most diverse group of birds in the Cretaceous world.

More than a decade later, Sanz and Buscalioni (1992) reported the first European records of Enantiornithes, describing several taxa such *Iberomesornis*, *Concornis*, and *Eoalulavis* from the Early Cretaceous of Spain in a subsequent series of papers (Sanz et al. 1996). Studies of other Mesozoic birds demonstrated that several Cretaceous avian taxa such as *Alexornis* from Baja California and *Gobipteryx* from Mongolia discovered earlier could be allocated to Enantiornithes (Martin 1995b). Moreover, these birds possessed not only a reverse scapulocoracoid joint but also other distinct features such as a unique formation of the triosseal canal in the shoulder joint, an unusual sternum, a humerus with a large hole in it, and warped foot bones where the metatarsals were fused proximally to distally, the opposite of that in modern birds. Other unique features in this group include projection of the third metacarpal farther distally than the second, a large posterior trochanter in the femur, and a narrow fourth metacarpal.

In addition to *Enantiornis*, other isolated bones of enantiornithines from El Brete were later allocated to different taxa such as *Soroavisaurus*, *Lectavis*, *Youngavolucris*, and *Martinavis* (Chiappe and Walker 2002). In the past two decades, Zhonghe Zhou of Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, and Luis Chiappe of Los Angeles County Museum have made valuable contributions to our knowledge of enantiornithine birds with their colleagues, describing dozens of new taxa from China, Spain, and Argentina, and establishing their phylogenetic relationships.

In China, a series of small, enantiornithine fossils have been discovered from the Early Cretaceous Jehol lakebeds, often with exquisite feather impressions that provide critical insights about anatomical transformations for flight improvement from the basal pygostylian condition. Enantiornithine specimens from Spain and

China, although frequently consisting of complete or near complete skeletons, are typically preserved in two dimensions, crushed flat, thus obscuring some of the anatomical details. In contrast, several enantiornithine birds from the Late Cretaceous deposits of North America, Europe, Mongolia, Madagascar, and Argentina, though incomplete, have provided three-dimensional anatomy, diverse adaptations, and a trend toward increased body size. Evolving from a *Confuciusornis*-like ancestor, enantiornithine birds became more cosmopolitan and widespread during the Late Cretaceous period.

Walker's recognition of Enantiornithes as a distinct lineage of Mesozoic birds was a great insight as more and more fossils were discovered from all over the world showing the same basic body plan. Before recognition of Enantiornithes as a distinctive Cretaceous clade, paleontologists had tried to piece together the later steps in bird evolution from the gliding *Archaeopteryx*-stage relying on 100-million-year-old fossils of water-dwelling, flightless hesperornithiform birds that provide little clue to the origin of flight. Discovery of enantiornithines was a paradigm shift in the study of Mesozoic avian evolution and the origin of flight as they filled in critical gaps with advanced flight adaptations. Enantiornithes has proved to be an abundant, diverse, and widespread group of Mesozoic birds far beyond the initial insight of Walker. Most of Mesozoic bird diversity comprises species that are part of two major lineages, Enantiornithes and Ornithuromorpha, of which Enantiornithes dominated the Cretaceous landscape. Several authors (Martin 1995b; Chiappe and Walker 2002; Chiappe 2007; Chiappe and Dyke 2007) provided an extended discussion of Enantiornithes from different parts of the world. In spite of their great diversity in the Cretaceous, the interrelationships among different species of enantiornithine birds remain highly speculative and unresolved.

There appears to be a distinctive dichotomy between enantiornithines and the ornithuromorphs; Luis Chiappe and Jorge Calvo accommodated both clades in a larger group called Ornithothoraces. These two groups were previously considered to differ significantly in morphology, flight, habitat, and physiology. Morphological evolution of these two groups has been thought previously to be largely parallel because of opposite types of shoulder joints. In this view, both groups acquired sophisticated powered flight independently by convergent evolution (Martin 1995b; Zhou and Zhang 2005). However, new discoveries of basal birds, particularly some recent finds from the Jehol Group, have substantially reduced the morphological gap. In both flight performance and bone histology, ornithuromorphs were more derived than the enantiornithines. The shoulder joints of both Enantiornithes and Ornithuromorpha are functionally similar; both are peg-and-socket joints that make the scapula and coracoid flexible during flapping flight, but the nature of articulation of the peg-and-socket joint is opposite between these two groups. In ornithuromorphs, the peg-and-socket joint is similar to the design of modern birds, where the scapular peg fits into the coracoidal socket, and three bones—the scapula, coracoid, and humerus—form the supracoracoideus pulley for the wing elevator muscle. In spite of the differences in the design of flight apparatus, phylogenetic study suggests that Enantiornithes share more derived morphologies with ornithuromorphs than previously recognized. Enantiornithes is considered a sister taxon to the more derived clade ornithuromorphs (Zhou et al. 2008).

Enantiornithes was the most diverse and dominant lineage of Mesozoic birds with more than sixty species during the Cretaceous period that occupied different niches. The early forms were small and mainly arboreal, perching birds. Through time they became larger and efficient fliers and explored different lifestyles and a diversity of habitats, filling in a gap of 60 million years. Some became aquatic swimmers, while others were waders like shorebirds. Some reverted to biplane wing configuration with the development of leg feathers similar to the condition in *Microraptor*; others became secondarily flightless. Some became toothless and developed horny beaks. Others became piscivorous.

Like the early radiation of other clades of birds, enantiornithines show a mosaic of primitive and derived avian characters. Derived characters are related to their improvement of flapping flight apparatus or perching

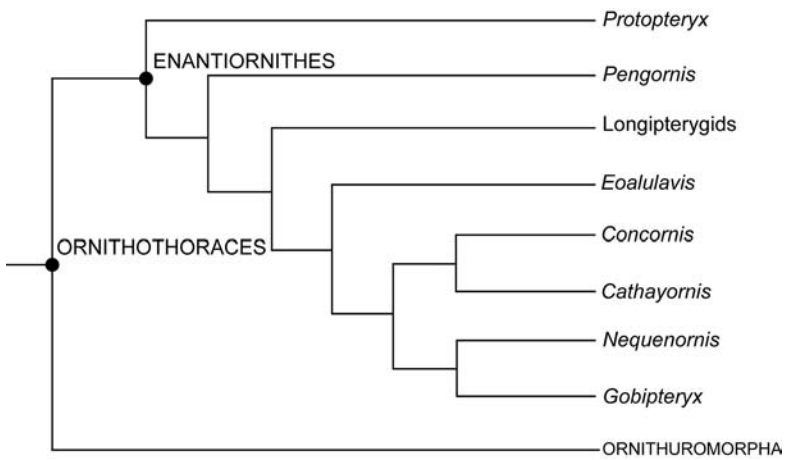


Figure 8.1. Cladogram showing the phylogenetic relationships of selected taxa of enantiornithine birds.

behavior, including a short and fused pygostyle, a broad sternum, a flexible scapulocoracoid joint with a strut-like coracoid, a spring-like furcula with a large hypocleidium, a wing-folding mechanism, large wings and flight muscles, an alula, and perching feet. In spite of their flight improvements, enantiornithines preserve striking primitive features such as a toothed snout in the skull, claw-tipped fingers, unfused pelvic elements, a footed pubis, and gastralia.

The majority of known species of Enantiornithes come from a select few localities in Spain, China, Argentina, and Mongolia. However, the phylogenetic relationships of Enantiornithes are in a state of flux and poorly resolved, partly because these birds are usually small, morphologically uniform, and often preserved in a flat slab of rocks in two dimensions, where many anatomical characters are difficult to interpret. Some of the selected taxa of enantiornithine birds are discussed below with their presumed phylogenetic relationships (fig. 8.1).

Las Hoyas Lagerstätten, Spain

The Early Cretaceous Las Hoyas fossiliferous deposits, though small and limited in areal extent, preserve many types of early enantiornithine birds. The outcrop of Las Hoyas occurs as a small pocket near the medieval town of Cuena in central Spain, consisting of about 20-meter-thick laminated limestone of the La Huerguina Formation. These fine-grained limestones, similar to the Solnhofen Limestone of Germany, were used for lithography or printmaking and contain abundant fossil remains of terrestrial and freshwater flora and fauna in exquisite detail that lived in and around an inland lake some 115 million years ago. The lake sediments are finely bedded horizontally without any disturbances, suggesting that it was a tranquil and low-energy environment so that organisms remained intact after death with little bioturbation. The bottom of the lake was probably anoxic (devoid of oxygen), thus preventing bacterial decay and increasing preservation potential. When the animals died and were buried at the bottom of the lake, the anoxic condition provided the ideal setting for fossilization and preservation of delicate carcasses, including soft tissues, high-degree articulation, and skeletal integrity. The birds from Las Hoyas made a significant contribution to our current understanding of the early evolutionary phases of enantiornithine flight capability. They show the improvement of the flight apparatus, including a strut-like coracoid; a modern, V-shaped furcula; a pygostyle; and the presence of an alula. Some of the enatiornithine birds from the Las Hoyas are described below.

Iberomesornis

This celebrated bird from the Las Hoyas of Spain is another significant fossil find linking *Confuciusornis* to later birds. Although the bird was reported briefly in 1988, J. L. Sanz and José Bonaparte formally named *Iberomesornis*

romeralli in 1992, when they analyzed its characters and compared it with other Mesozoic birds (fig. 8.2B). The specimen was found in a lacustrine or lagoonal deposit of lithographic limestone that has yielded several avian specimens, an isolated feather, and a diversified flora and fauna. *Iberomesornis* is based on a partial skeleton missing the skull, anterior cervical vertebrae, carpus, and manus. It is articulated but badly crushed. This sparrow-sized bird, about 8 centimeters long, is similar in many ways to *Sinornis* of China (fig. 8.2A) and shows a combination of primitive and advanced characters. The coracoid is typically avian—strut-like with an acrocoracoid process and an expanded distal end for the connection with the sternum. There is an ossified and probably keeled sternum. The furcula is spring-like and narrow, ending with a large hypocleidium. The humerus has a stout deltopectoral crest and a well-defined ligamental groove. The tail is short, with the development of a pygostyle. *Iberomesornis* was obviously well adapted for powered flight. Unlike in *Sinornis,* gastralia is not found in *Iberomesornis.* The cervical vertebrae show low neural spines but lack heterocoely and hypapophyses. The pelvis, sacrum, and hindlimb are primitively built in the fashion of *Archaeopteryx*. The foot is anisodactyl, and the hallux claw is very large. Martin (1995b) included *Iberomesornis* within enantiornithine birds.

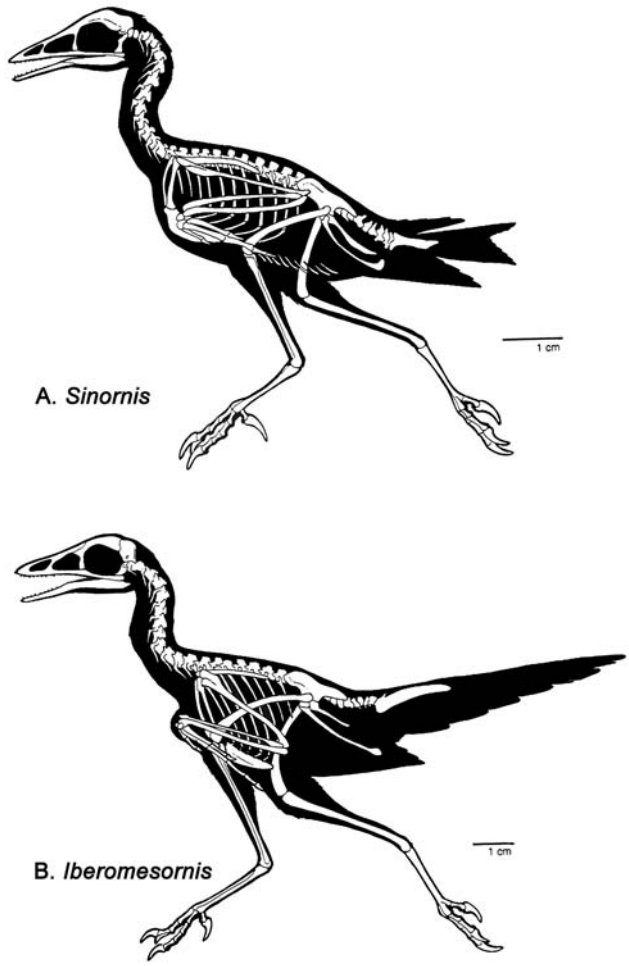


Figure 8.2. Early Cretaceous enantiornithine birds. A, skeletal reconstruction of *Sinornis santensis* from the Liaoning Province of northern China. B, skeletal reconstruction of *Iberomesornis romeralli*, a basal enantiornithine bird from the Early Cretaceous La Huerguina Formation of Las Hoyas, Spain (after Chatterjee 1997).

Concornis

J. L. Sanz and A. D. Buscalioni (1992) described a second bird, *Concornis lacustris*, from the same horizon of Las Hoyas of Spain. *Concornis* shows an asymmetrical feather impression, but the specimen lacks the skull. *Concornis* is twice the size of *Iberomesornis*, but its anatomy is poorly known. The flight apparatus is very similar to that of *Iberomesornis*, with a strut-like coracoid, a hypocleidium-bearing furcula, and a keeled sternum, all collectively indicating an advanced level of flight ability. *Concornis* seems to be more derived than *Iberomesornis* because it has a fused tibiotarsus and shows a trochlear surface on the distal end of the metatarsus. Larry Martin (1995b) has allied the Chinese and Spanish birds with Enantiornithes.

Eoalulavis

Sanz et al. (1996) reported another new enantiornithine bird, *Eoalulavis hoyasi*, from the Lower Cretaceous Las Hoyas of Spain. The skeletal wingspan of this bird is 17 centimeters, about the size of a goldfinch's. The outstanding feature of this skeleton is the preservation of the alula, or bastard wing, indicating that this bird could fly at slower speed and attained maneuvering flight 115 million years ago. The stomach contents suggest that *Eoalulavis* probably subsisted on crustaceans.

The Jehol Enantiornithes from China

The Jehol biota has the most species-rich group of enantiornithine birds, which were small, numerous, and adapted to arboreal environments as reflected by their perching feet. New species of enantiornithines showing a wide range of morphological and ecological variation are being discovered from the Jehol Group at an unprecedented rate. Despite tooth reduction in Chinese avialans and pygostylians, the enantiornithines typically possessed full sets of teeth, which are small, slightly recurved, and unserrated. Some possessed bulbous teeth for cracking hard food objects. Others would become edentulous. Some would develop highly elongated jaws for probing food. A wide range of tooth morphologies and dental patterns indicates that Enantiornithes adapted a wide range of dietary habits.

The Chinese enantiornithines are remarkable for their diversity. During the past two decades, about sixty species of new birds have been named from the Jehol Group; more than half of these species are referable to Enantiornithes that are represented by partial or articulated skeletons, often preserving impressions of feathers in exquisite detail. These enantiornithines coexisted and competed with a variety of theropods and early birds in the Jehol ecosystems. No doubt some of these enantiornithines became occasional victims of other arboral theropods as reflected by their stomach contents. The predator in this case was the fearsome arboreal raptor, *Microraptor gui* with biplane wing configuration. A recently discovered articulated skeleton of *Microraptor* has revealed remains of an adult enantiornithine bird preserved in its stomach contents. As the ingested bird was still articulated, the prey was most likely not scavenged but captured and consumed by the dromaeosaurid (O'Connor et al. 2012). No doubt *Microraptor* fed on arboreal birds and spent considerable time in trees using stealth attack to capture birds.

Some of the enantiornithine birds that figure prominently in morphology, phylogeny, and radiation in the Jehol ecology are described below.

Protopteryx

The earliest record of enantiornithine birds is *Protopteryx fengningensis* from the lowest unit of the Jehol Group, the Dabeigou Formation (about 130 million years old) at the Senjitu locality near Fengning, Hebei Province (Zhang and Zhou 2000). This small, toothed bird, about the size of a starling, is perhaps the most primitive known enantiornithine, reflected by its long hand and digit 1, and unfused carpometacarpus and tibiotarsus (fig. 8.3A). The hands retained claws and the phalangeal formula is 1-3-2-x-x. The skull is crushed with a pointed snout bearing few conical and unserrated teeth in the premaxilla and dentary. The orbit is large with an expanded braincase. The quadrate head is single with a flexible otic joint. However, *Protopteryx* had developed several flight-related advanced features including the alula, or bastard wing, as in *Eoalulavis*, which is attached to the unreduced alular or first digit. The sternum is wide with an incipient keel, the furcula has a large hypocleidium, and the coracoid has a procoracoid process to form a triosseal canal that would help to raise the wing in flight with a pulley mechanism. The two long tail feathers are scale-like without branching as in the red bird of paradise, perhaps used for sexual display. From these initial stages of the body plan, as represented by *Protopteryx*, enantiornithines show a sudden explosive radiation of shapes, sizes, and habitats.

Pengornis

Pengornis houi is the largest known enantiornithine bird from the Early Cretaceous Jiufotang Formation of China, based on a single but exquisite fossil skeleton with a beautiful intact skull (fig. 8.3B) (Zhou et al. 2008). It is a crow-sized bird, comparable to *Confuciusornis* in size and proportion, but significantly larger than all previously described early Cretaceous enantiornithines. The skull has a primitive bird-like design similar to that of *Cathayornis* with a narrow tooth-bearing snout, a large external naris, a small and triangular antorbital fenestra, a dome-shaped roof, an inflated braincase, a large orbit, a modified diapsid temporal configuration, a narrow jugal bar,

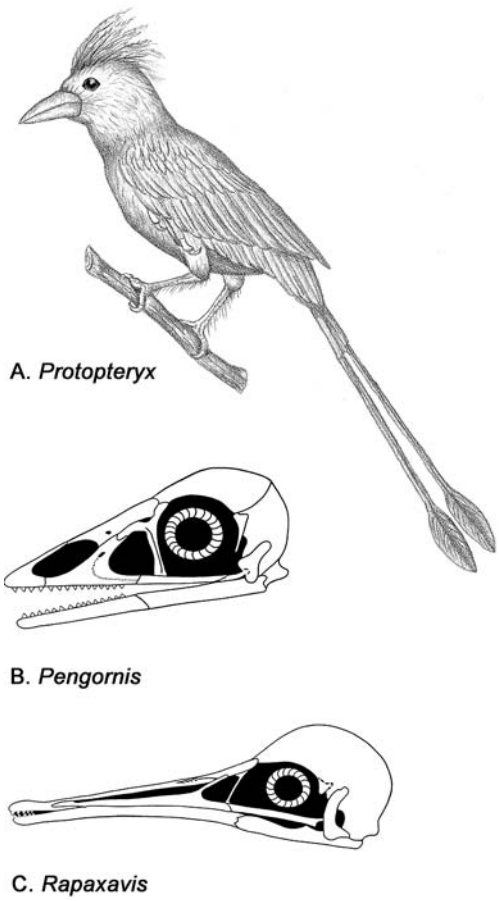


Figure 8.3. Basal Enantiornithes from the Early Cretaceous of China. A, life restoration of *Protopteryx fengningensis*. B, restoration of the skull of *Pengornis houi* showing a modified diapsid condition (modified from O'Connor and Chiappe 2011). C, restoration of the skull of *Rapaxavis pani* depicting a modified diapsid condition and longirostral jaws (modified from O'Connor and Chiappe 2011).

and a postorbital-jugal bar. The quadrate appears to be single-headed as in *Cathayornis* and fits into a socket of the squamosal, forming a flexible otic joint. The loss of the squamosal-quadratojugal bar and the ascending process of the jugal clearly suggest that the quadrate is streptostylic. The premaxillae are unfused; the nasal meet on the midline to exclude the premaxillae from contacting the frontals, indicating that the craniofacial flexion zone was probably not developed at this stage. In ornithurine birds, the premaxillae contact the frontals, thus displacing the nasals laterally to form the prokinetic hinge. Most likely, *Pengornis* achieved some degree of primitive cranial kinesis (see chapter 15). Most of the teeth are small and conical, with blunt crowns and constricted waists, but those toward the back are globular and blunt with wear facets, probably used for cracking hard objects. There are about thirteen teeth in the dentary and a similar dental count is expected in the upper jaw.

There are about eleven cervical vertebrae; the anterior ones show heterocoelous centra, but the posterior ones are amphicoelous. There are seven fused sacrals forming the synsacrum with the ilium. The scapula has a large and recurved acromion process as in ornithurine birds. The coracoid is strut-like but lacks the procoracoid process. It is slightly expanded at its sternal end. The furcula is V-shaped, but most of the hypocleidium is missing. The forelimb is significantly longer than the hindlimb with a ratio of 1.35. The humerus has an oblate, globose head as seen in ornithurine birds. The ulna is considerably longer than the humerus. Major (II) and minor (III) metacarpals are fused proximally with the semilunate carpal to form the carpometacarpus. The pelvis is incompletely preserved. The femur is bowed and slightly shorter than the tibiotarsus. The distal tarsals are fused to each other and to the proximal metatarsals to form a tarsometatarsus, which remains unfused distally.

Pengornis plays a crucial role in resolving the dichotomy between enantiornithines and ornithuromorphs because it possesses several characters that were previously thought to be limited to ornithurine birds, including the development of kinesis, heterocoelous cervical vertebrae, a hooked acromion, a globular humeral head, and an ulna longer than the humerus. Most likely these characters evolved earlier in enantiornithine birds than hitherto recognized, indicating the close phylogenetic relationships between enantiornithines and ornithuromorphs.

Rapaxavis

One of the unusual trends in Jehol Enantiornithes was the development of a long bill (longirostral jaws)—longer than the rest of the skull—with few hooked teeth at the

tip, which was designed for probing feeding behavior, somewhat the ecological equivalent of that of a modern kingfisher. So far five genera of longirostral enantiornithines are known from the Early Cretaceous of China, including *Longipteryx*, *Longirostravis*, *Rapaxavis*, *Shanweiniao*, and *Boluochia*, which are grouped in the family Longipterygidae. Of these *Longipteryx*, *Longirostravis*, and *Shanweiniao* are known from the older Yixian Formation, whereas *Boluochia* and *Rapaxavis* are from the younger Jiufotang Formation of China, suggesting that longipterygids diversified during a span of about 5 million years. These birds represent a new ecological radiation with the development of a long and slender beak for catching fish with restricted teeth at the tips of the jaws or probing in the mud, perhaps exploiting new aquatic food resources, a departure from all known members of Enantiornithes. The elongation of the rostrum of this lineage facilitated greater diversification and ecological dominance of longipterygids among enantiornithines in the aquatic realm of Jehol biota, as represented by five taxa with a wide range of dental and pedal morphologies that suggest subtle differences in niche partitioning and food preferences. Most likely, the primary foraging areas for the longipterygids were the numerous lakes in the Jehol environment, stocked with abundant fish and invertebrates. Longipterygids would perch on trees overlooking these foraging areas and would land on the lake surface for feeding during most of the day, but fly back to the trees during the night for resting, sleeping, and nesting.

Among these longipterygids, *Rapaxavis pani* is one of the most complete enantiornithine specimens described to date and provides a wealth of anatomical information (Morschhauser et al. 2009; O'Connor et al. 2011). The taxon is based on a solitary specimen, where the skeleton is exposed in the ventral aspect. The unusual feature in *Rapaxavis* skeleton is that some distal limb elements remain unfused, which might indicate either an immature individual or primitive morphologies. Another unusual feature of this taxon is the preservation of a pair of bizarre bones, paracoarcoidal ossifications, dorsal to the coracoid-sternum articulation that might be linked to an additional attachment area for flight muscles.

The skull is crushed but shows a long, tapering, and ventrally concave rostrum (fig. 8.3C). The premaxilla has a long nasal process to contact the nasal. It supports three teeth at the tip that rapidly decrease in size from front to back. The maxilla is toothless and forms the major component of the facial margin. The outstanding feature of the skull is the development of a slit-like (schizorhinal) naris as in modern rhynchokinetic birds to flex the upper beak, a feature associated with probing adaptation. The orbit and postorbital regions are poorly preserved. The quadrate appears to be single-headed. The dentaries possess an unfused mandibular symphysis and two teeth at the tips.

There are eight or nine cervicals that show lateral excavation. Other bones conceal most of the thoracic vertebrae but ten thoracic ribs are visible. The sacrum has a lower count and consists of six fused vertebrae. There are six free caudals, followed by a long, stout pygostyle. Gastralia are preserved near the pelvic girdle. The scapula is a narrow blade but shows a robust acromion process. The coracoid is strut-like, expanded distally at the sternal contact, but lacks the procoracoid process in the proximal end. The dorsal surface appears to be slightly excavated. The furcula, preserved between the two coracoids, is Y-shaped and bears an elongated hypocleidium. The sternum is quadrangular; the rostral margin receives the coracoid at an obtuse angle. It has two lateral and one medial xiphoid processes that project considerably backward; the caudal margin forms a wide V and supports six or seven sternal ribs. The sternum bears a short ventral ridge, probably an incipient keel. The humerus is long and twisted at its ends in relation to the shaft. The proximal head is saddle-shaped; distal to the head, a low but distinct deltopectoral crest projects craniolaterally. The bicipital crest is prominent, forming a cranial projection relative to the shaft. Distally, the dorsal condyle is smaller than the ventral. The ulna is robust and subequal to the humerus, and is gently bowed proximally near the humeral articulation. Distally, it articulates with the ulnare. The radius is a slender element. The highly derived manus, which is shorter than the ulna, lacks unguals and has a phalangeal formula of 1-2-2-x-x, indicating digital

reduction. The carpometacarpus is partially fused proximally. The reduction of the manus might have increased aerodynamic capabilities of *Rapaxavis* by streamlining the wing, strengthening the hand for primary feathers, and decreasing weight.

The pelvic girdle is disarticulated. The preacetabular process of the ilium has a broad, rounded cranial margin; the postacetabular process is short and narrow. The ischium is long, two-thirds the length of the pubis. Proximally, it has a stout dorsal process. In the acetabular component, the iliac peduncle is narrow and longer than the broad pubic peduncle. The pubis is rod-like, retroverted with a pubic foot, and is unfused at the distal symphysis. The femur is shorter than the tibia, and bowed craniodorsally. The femoral head is separated from the shaft by a distinct neck. The tibiotarsus remains unfused unlike in other enantiornithines, where the proximal tarsals are fused to each other but not to the tibia. The fibula is reduced and splint-like distally. The distal tarsals are unfused with the metatarsals unlike the condition of other enantiornithines. The metatarsals are fused proximally but remain separate distally. The pes shows perching ability and arboreal adaptation with highly recurved claws encased in long horny sheaths; the phalangeal formula is 2-3-4-5-0.

Sinornis

In 1992, Paul Sereno and Chenggang Rao described a sparrow-sized bird, *Sinornis santensis*, from the Early Cretaceous lake sediments of Liaoning Province of northern China (fig. 8.3A). *Sinornis* appeared about 10 million years later than *Archaeopteryx* and shows a great deal of modification in the flight apparatus. The skull is virtually unknown except for tooth-bearing jaws. The postcranial skeleton of *Sinornis*, like that of *Archaeopteryx*, shows several primitive features, such as an unfused carpus and metacarpus, a clawed manus, separate pelvic bones, a footed pubis, separate metatarsals, gastralia, and limited skeletal fusion. However, the flight apparatus is more advanced than that of *Archaeopteryx*. *Sinornis* appears to have a strut-like coracoid; a furcula with elongate hypocleidium; and a broad, ossified sternum. The laterally facing glenoid permitted dorsoventral movement of the humerus during flight. The wrist joint is modified by the development of a large radiale and complex ulnare, which would interlock the short manus in place during the flight stroke. The finger bones are separate and the claws are reduced. The thorax is short, and the tail is truncated, with only eight free vertebrae and a large pygostyle. No doubt *Sinornis* was capable of powered flight. The pes shows a fully reversed hallux and highly recurved claws, indicating a perching adaptation and arboreal habitat. *Sinornis* is currently grouped with enantiornithine birds.

Cathayornis

In 1992, soon after the discovery of *Sinornis*, three Chinese colleagues, Zhou Zhong, Jin Fan, and Zhang Jiang, reported another small bird, *Cathayornis yandica*, from the Early Cretaceous lakebeds of the Jiufotang Formation of northern China. Two well-preserved postcranial skeletons provide critical anatomical information on *Cathayornis*. Zhou (1995a) gave a more detailed description of *Cathayornis* in a subsequent paper. The reverse scapulocoracoid articulation, broad furcular arms, the anterodorsal ischial process, and proximal to distal metatarsal fusion indicate its affinity with enantiornithine birds.

The skull is well preserved in the side view, showing a toothed beak (fig. 15.10C). The premaxillae are probably fused along the midline. As in modern birds, the frontal bones are enlarged, the parietal is reduced, and the supraoccipital abuts against the parietal. The foramen magnum has been shifted ventrally. The temporal configuration has been modified considerably so that the large circular becomes confluent with the lower temporal opening. The quadrate seems to have an orbital recess and developed streptostyly with the loss of the squamosal-quadratojugal bar. Most likely *Cathayornis* developed a primitive form of cranial kinesis (see chapter 15). Like *Sinornis*, *Cathayornis* is a small perching bird with advanced flight adaptations, such as a strut-like coracoid, a V-shaped furcula, a keeled sternum, a swivel wrist joint, and a pygostyle. The synsacrum has eight fused vertebrae. The carpometacarpus, pelvic bones, and metatarsals remain separate. The

humerus lacks a bicipital crest, and the hindlimb is primitively built in the fashion of *Sinornis*. The pubis has a foot, as seen in *Sinornis*.

Morphologically, *Cathayornis* is very similar to *Sinornis*, and their taxonomy and synonymy remain controversial. Several authors have proposed that *Cathayornis yandica* is a junior synonym of *Sinornis santensis*. There are several reasons for this taxonomic confusion because of poor preservation of holotype specimens. Both taxa are small, sparrow-sized birds, comparable in size and mode of preservation in which the bones are preserved as natural molds in slabs and counterslabs. Since bones are not preserved, previous studies are based on cast skeletons. Recent work suggests that *Sinornis* and *Cathayornis* are two distinctive taxa; both show clear and distinctive and anatomical differences in hand, pelvis, and pygostyle morphology to justify separating these two taxa (O'Connor and Dyke 2010).

Upper Cretaceous Enantiornithes from China

Recently, a small, Late Cretaceous enantiornithine bird, *Paravis chuxiongensis*, has been reported from the Jiangdihe Formation from southern China based on an incomplete skeleton (Wang et al. 2014). The diagnostic features of this species are found in the foot morphology, where metatarsals II and IV terminate proximal to the entire trochlea of metatarsal III. Discovery of *Paravis* extends the temporal and geographic range of Mesozoic birds in China.

Enantiornithes from Argentina

During the Late Cretaceous, between 84 and 65 million years ago, the continents continued to separate and began to assume the positions of the present day. Great warm seas covered much of the Earth during this period, a time of mild climate and ice-free polar regions. The Western Interior Seaway, almost 1,500 kilometers wide, at times bisected the North American continent. The western shore of the interior sea was inhabited by many species of diving birds and shorebirds. Many terrestrial birds and bird-like forms thrived in South America and Mongolia.

Several taxa of enantiornithines are known from the Late Cretaceous deposits of Argentina, including *Enantiornis*, *Neuquenornis*, *Yungavolcuris*, *Lectavis*, *Intiornis*, and *Soroavisaurus*. Many of taxa of are based on an abundant assortment of mostly disarticulated postcranial elements from the Late Cretaceous Lecho Formation of El Brete, except for *Neuquenornis*, which is represented by an articulated specimen from Patagonia and provides valuable information about the anatomy of the Late Cretaceous enantiornithine birds.

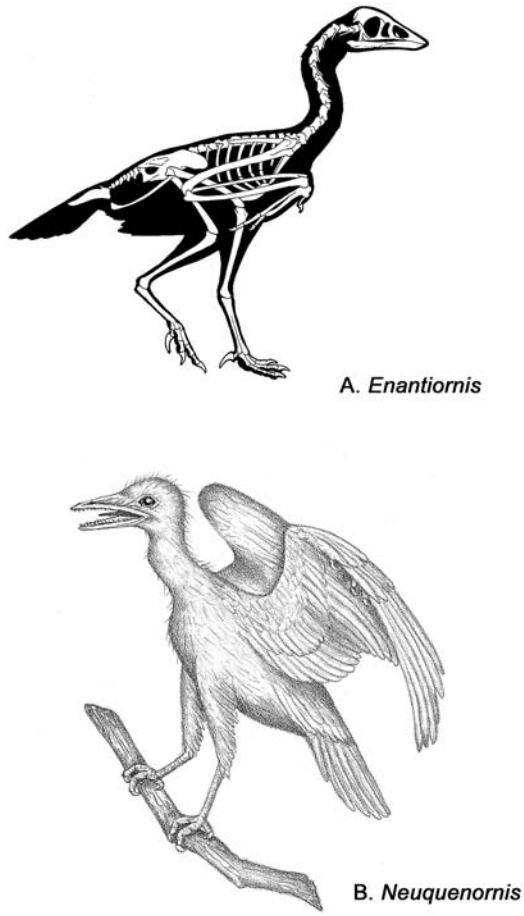


Figure 8.4. Derived Enantiornithes from the Late Cretaceous of Argentina. A, skeletal reconstruction of the first-described species of enantiornithine birds, *Enantiornis leali* (after Chatterjee 1997). B, *Neuquenornis volans* from the Late Cretaceous Rio Colorado Formation of Patagonia, Argentina.

Enantiornis

Cyril Walker first described *Enantiornis leali* from the Late Cretaceous Lecho Formation of Argentina in 1981 on

the basis of isolated elements. Walker recognized novel morphologies of this species and erected a new subclass, Enantiornithes. *Enantiornis* was among the largest enantiornithine birds, resembling a turkey vulture in size and habits with a wingspan of 1.2 meters (fig. 8.4A).

Neuquenornis

The falcon-sized *Neuquenornis volans* is known from an articulated specimen including the posterior portion of the skull, five thoracic vertebrae, wings, a shoulder girdle, a partial sternum, a furcula, and partial hindlimbs (fig. 8.4B). This 80-million-year-old specimen was recovered from the Late Cretaceous fluvial deposits of the Rio Colorado Formation of northwestern Patagonia (Chiappe and Calvo 1994). The occiput of the skull shows a dome-shaped frontoparietal region to accommodate a large cerebellum. The braincase is fused and the foramen magnum is large compared to the occipital condyle in modern birds. In Early Cretaceous enantiornithines, the reverse is the case; the braincase bones do not fuse and the foramen magnum is proportionately smaller relative to the occipital condyle. The preserved thoracic vertebrae do not show any sign of heterocoely. The coracoid is strut-like; it lacks both the procoracoid and lateral processes and contains a deep triangular fossa on the dorsal surface, a hallmark of enantiornithine birds. The two bones are firmly articulated with the sternum and lie close to each other. Unlike in Early Cretaceous enantiornithines, the sternum of *Neuquenornis* has a prominent keel that projects cranially beyond the sternocoracoid articulation, indicating the presence of large flight muscles. The humerus is slender and shorter than the ulna. The carpometacarpus is fused proximally and the extensor process is small and rounded. Metacarpal II and metacarpal III are robust and of subequal length. The femur is long and slender and arches dorsally; it is shorter than the humerus. The metatarsals are fused proximally but closely apposed distally. Metatarsal III is the longest, metatarsal II and metatarsal III are robust, but metatarsal IV is highly reduced. Metatarsal I is J-shaped and digit 1 is reverted, indicating that *Neuquenornis* was able to perch. *Neuquenornis* is currently placed in a distinct family Avisauridae along with other enantiornithines such as *Soroavisaurus* and *Avisaurus*. Recently, avian eggs with partially articulated embryonic skeletons have been found from the Rio Colorado Formation of Argentina, which are tentatively allied to *Neuquenornis*.

Enantiornithes from Mongolia

The Late Cretaceous continental sediments of the Gobi Desert of Mongolia are famous for their spectacular dinosaur fossils, but in recent times small but interesting bird fossils—both enatiornithines and ornithuromorphs—have been discovered from two successive horizons: Barun Goyot and Djadokhta Formations of Campanian age, and Nemegt Formation of Maastrichtian age. These two horizons have been considered to represent at least two distinct Late Cretaceous environments and vertebrate faunal zones. The spectacular orange-red sediments of the Barun Goyot and Djadokhta Formations were deposited in an arid environment and have yielded protoceratopsids, armored ankylosaurs, lizards, and mammals, but the overlying Nemegt beds were laid down under more humid conditions and have produced massive dinosaurs such as hadrosaurs, sauropods, and tyrannosaurs. Similar to dinosaur distributions, these two horizons tend to show two distinct avialan assemblages: the lower two formations, Barun Goyot and Djadokhta, are dominated by enantiornithine birds such as *Gobipteryx*, *Gobipipus*, and *Elsornis*, as well as a solitary ornithuromorph bird *Asparavis*. Among enantiornithines, *Elsornis* became a secondarily flightless bird (Chiappe et al. 2007). Ornithuromorphs are more common in the overlying Nemegt Formation, represented by various taxa of Hesperornithes; a derived bird, *Teviornis*; and several unnamed taxa.

Gobipteryx

Elzanowski (1981) described several precocial embryonic skeletons of *Gobipteryx minuta*, found preserved still within their eggs, from the Late Cretaceous Barun Goyot Formation of Khermeen Tsav in the southern Gobi Desert of Mongolia. He classified *Gobipteryx* as a primitive palaeognathous bird, distantly related to modern flightless birds such as ostriches and emus. However, in embryonic

specimens of *Gobipteryx*, many adult characters were not fully expressed, thus making its classification more difficult. Martin (1995b) correctly assigned *Gobipteryx* to enantiornithine birds and received independent support from other studies. Chiappe et al. (2002) described a beautifully preserved adult skull of *Gobipteryx minuta* from the same horizon of Mongolia. On the basis of this new skull, they synonymized *Gobipteryx minuta* with *Nanantius valifanovi*, another adult skeleton of an enantiornithine bird described previously by the Russian paleontologist Evgeny Kurochkin (1996) from the same horizon. Thus *Nanantius* becomes a junior synonym of *Gobipteryx*, and it supplements critical anatomical information on *Gobipteryx* and its enantiornithine relationship, which was largely lacking in embryonic skeletons. Among enantiorithine birds, both *Gobipteryx* and *Gobipipus* were completely toothless. These birds were about the size of a crow, approximately 35 to 40 centimeters long (fig. 8.5).

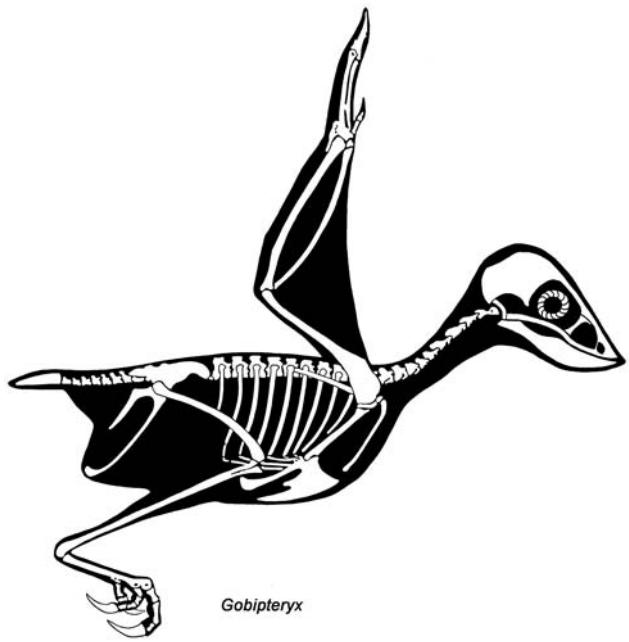


Figure 8.5. Derived Enantiornithes from the Late Cretaceous Barun Goyot Formation of the Gobi Desert, Mongolia. Skeletal restoration of *Gobipteryx minuta* (Kurochkin 1996; Chiappe et al. 2001).

The skull of *Gobipteryx* is incompletely preserved. The fused premaxillae form the broad and upturned rostrum without a hook. The external naris is teardrop-shaped with its main axis directed anteroventrally. Unlike in other enantiornithines, the maxillary fenestrae are absent in *Gobipteryx*, and the nasal processes of the maxillae are reduced. The orbit is round and large, covered with a sclerotic ring. *Gobipteryx* provided critical information about palatal morphology, which is otherwise poorly known in enantiornithine birds. The palate is quite different from palaeognathous conformation and shows a maniraptoran-like bauplan. The palate is vaulted with backward migration of the choanae. The premaxillae are fused to form a secondary palate, which is interrupted by a large horseshoe-shaped palatal chamber that connects the oral cavity with the large chamber of the palatal vault. Behind the chamber lie small and paired choanae, separated by fused rod-like vomers that fail to reach premaxillae anteriorly and pterygoids posteriorly. The vomers are fused throughout in their anterior half, but are split backward to contact the palatines laterally. The palatine is long and paddle-like, articulating with the vomer anteriorly and the pterygoid posteriorly. The pterygoid is robust, forked anteriorly to connect the palatine and ectopterygoid; the latter bone is hooked to connect the jugal and makes the palate firm and immobile. The dorsal quadrate head is single and has a broad pterygoid ramus as in theropods without any development of a true orbital process; distally, the quadrate is bicondylar for articulation with the mandible. The mandibles are low and straight, fused to each other at the symphysis, and show a series of nutrient foramina on the lateral surface of the dentary.

The postcranial skeleton shows several hallmarks of enantiornithine birds. The scapula is robust and straight with a well-developed acromion. The coracoid is long and slender with a broad triangular fossa on the dorsal surface. The scapular articular facet is convex; the acrocoracoid process is subdued. The coracoid shaft is expanded and is pierced by a large supracoracoid nerve foramen. Distally, the coracoid expands and articulates close to each other on the sternum. The humeral head is concave anteriorly and convex posteriorly with a prominent bicipital crest. The deltopectoral crest is flat

and broad. Distally, the humerus is compressed and the articular condyles are poorly developed. The ulna is as long as the humerus.

Gobipipus

Gobipipus reshetovi, another sympatric species of *Gobipteryx minuta*, is known from the Barun Goyot Formation of the Gobi Desert of Mongolia (Kurochkin et al. 2013). *Gobipteryx* is described in chapter 13 because of its embryonic development along with its eggs (see fig. 13.5). Two embryonic skeletons, enclosed inside the eggs, represent *Gobipipus*, where many of the adult characters were not fully expressed. However, *Gobipipus* is anatomically quite distinct from the embryonic *Gobipteryx* in the structure of the skull, the flight apparatus, and the relative size of the neural canal in the vertebrae. Also, morphology of eggs between these two genera is quite distinctive.

The skull of *Gobipipus* is relatively small, with an upturned and toothless beak. The flight apparatus suggests that *Gobipipus* was an acrobatic flier. The well-ossified skeletons of *Gobipipus* indicate its precocial mode of development; the hatchlings could walk away from the ground nests as soon as they emerged from their eggs and possibly could fly. *Gobipipus* is discussed separately in chapter 13 on eggs and embryos.

Lifestyle of Enantiornithes

The diverse enantiornithine birds with more than sixty taxa spanned most of the Cretaceous period (120–65 million years ago), and have been recorded from all continents except Antarctica (Chiappe and Walker 2002). Because of their long geologic range and wide geographic distribution in diverse habitats, we can speculate about their inferred ecology, nesting behavior, and growth strategies. Most enantiornithine fossils occur in continental sediments of fluvial, eolian, or lacustrine environments, indicating their preference for terrestrial habitats. Their fossils have been found from the tropics to the polar regions, suggesting their adaptation in wide range of latitudinal and climatic belts. Some enantiornithine taxa such as *Halimornis* from Alabama, *Nanantius* from Australia, and *Enantiophoenix* from Lebanon have been recorded in marine environments, suggesting that these birds occasionally ventured into the seas. They must have radiated rapidly to occupy the new flight niches with a high degree of maneuverability that enabled them to occupy a wide range of habitats.

Adaptive Radiation

The Early Cretaceous forms such as *Protopteryx*, *Pengornis*, *Iberomesornis*, *Concornis*, *Eoalulavis*, *Sinornis*, and *Cathayornis* were small, ranging in size between a sparrow and a thrush; many were arboreal, the ecological equivalent to living passeriforms or songbirds. From these initial stages of arboreal lifestyles, enantiornithines exhibit a tremendous diversity of shapes and sizes, concomitant with gradual improvement of flight adaptation.

There is a trend toward increasing body size in the Late Cretaceous forms, some of which became the size of a turkey vulture with wingspans reaching 1.5 meters. At this time, they became superb fliers that migrated across large oceans as Pangea was rifted and drifted apart. Their fossils have been found across the globe in several localities of Canada, the United States, Mexico, China, Mongolia, Uzbekistan, Russia, Hungary, France, Romania, Lebanon, Madagascar, and Argentina. Flightlessness also appears in Enantiornithes. *Elsoronis keni* from the Late Cretaceous of the Gobi Desert became secondarily flightless (Chiappe et al. 2007). The diversification of enantiornithines continued until the very end of the Cretaceous period, when they were wiped out entirely at the KT extinction. Yet the devastation caused by the extinction of enantiornithines and other ornithuromorphs also provided evolutionary opportunities for modern birds to undergo remarkable adaptive radiations.

Food Preferences

Given the wide diversity of skull shape and foot morphology, many dietary specializations must have been present among Enantiornithes. The forest habitat must have played a key role in the early radiation of enantiornithine birds and their diet. The anatomy of both skull

and feet hints at the presumed lifestyles of enantiornithine birds. The Early Cretaceous enantiornithines were as small as sparrows with short, toothed jaws and wide gaping mouths that were well suited for catching insects in the trees. They developed a primitive form of cranial kinesis that allowed a wide gape for swallowing a large amount of food. Their highly recurved pedal claws and anisodactyly indicate their perching and grasping ability. The short, blunt teeth of *Pengornis* were likely used to feed on soft-bodied arthropods. Many of these birds were partly ground dwelling, presumably for feeding, and partly tree-dwelling for perching, hiding, nesting, and sleeping. Through time, Enantiornithes developed a wide range of feeding adaptations. Although most of them were arboreal, some became swimmers, and others became long-legged waders; some developed long jaws, while others became edentulous. Stomach contents of some enantiornithines such as *Eoalulavis* from Spain suggest that at least some members of the group were aquatic feeders subsisting on crustaceans (Sanz et al. 1996). Some of the early enantiornithine birds had sharp and recurved teeth for catching slippery fish. They would congregate during the day on the open waters of rivers and lakes for foraging but fly up to the trees during the night for safety. *Longipteryx chaoyangensis* probably used its long rostrum with grasping teeth at the front for capturing fish like living kingfishers (fig. 8.6), whereas the gently curved long rostrum of *Longirostravis* was employed for mud probing like today's charadriiforms. In contrast, another long-jawed enantiornithine, *Rapaxavis*, was habitually arboreal as reflected by its well-developed perching foot; it probably probed in bark and other tree crevices like woodcreepers.

Late Cretaceous enantiornithines were generally larger. *Gobipteryx* was the size of a crow and *Enantiornis* was as large as a turkey vulture with a wingspan of 1.2 meters. The large Enantiornithes from El Brete of Argentina show a wide range of adaptive radiation (Chiappe 2007). The grasping feet with sharp claws of *Soroavisaurus* could be used as formidable weapons for seizing and slashing prey. The long and slender hindlimb elements such as the tibiotarsus, tarsometatarsus, and feet of *Lectavis* indicate wading adaptation in marshes, swamps, mud flats, and shallow bodies of water; the short, broad, asymmetrical, and divergent feet of *Yungavolucris* hint at its swimming adaptation. In toothless forms such as *Gobipteryx* and *Gobipipus* from Mongolia their broad and robust beaks were adapted for cracking hard objects like seeds or shelled invertebrates. *Enantiophoenix* from the Late Cretaceous marine limestone of Lebanon probably fed on the sweet sap of trees like modern sapsuckers because tiny pieces of amber have been recovered between its bones and feathers as food particles (Chiappe 2007).

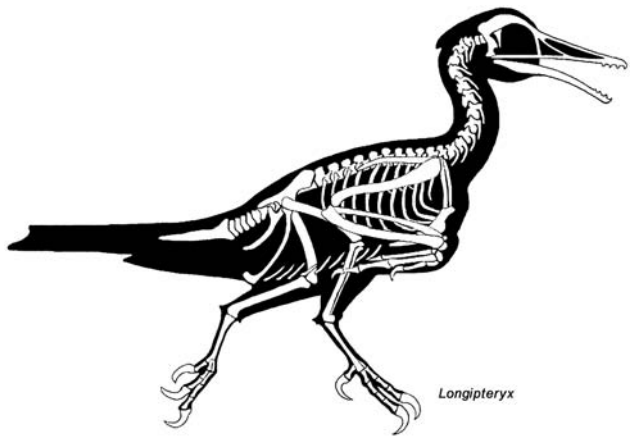


Figure 8.6. Restoration of the skeleton of *Longipteryx chaoyangensis* from the Early Cretaceous of China with elongated rostrum and anterior teeth. This bird was probably adapted for capturing fish with its long jaws like those of the modern kingfisher (modified from Chiappe 2007).

Nesting Behavior

Like modern birds, enantiornithines laid eggs, and perhaps in nesting sites, but we know very little about their reproductive behavior. Just as an aircraft cannot fly if it is overweight, all female birds must dispense with fertile eggs as soon as they are formed. Finding a safe place to hatch their eggs to avoid detection of predators was a challenge to enantiornithine birds amid hungry theropods. Since early enatiornithines were largely arboreal, they possibly laid eggs in inconspicuous nests in trees for safety and protection; however, the preservation of arboreal nests in the fossil record would be extremely limited.

Some enantiornithines laid their eggs directly on the

ground as revealed from the fossil record. Smaller birds tend to lay relatively small eggs compared to large species. This is why eggs of enantiornithine birds were generally small and ovoid, ranging in size from 35 to 45 millimeters long, and 20 to 27 millimeters wide. Though most birds nest individually, many species gather together in large colonies during breeding seasons. So far, two spectacular nesting sites of enantiornithine birds that formed enormous breeding colonies have been discovered, one from the Gobi Desert of Mongolia and the other from Romania. The eggs from the Gobi Desert often contain embryonic remains of precocial birds with ossified skeletons such as *Gobipteryx* and *Gobipipus* (see chapter 13). In addition, enantiornithine eggs with precocial embryos have been reported from Argentina and China. Apparently, hatchlings of enantiornithine birds were completely self-sufficient with precocial development; they were able to walk, fly, feed, and generally look after themselves with little parental care within a day or even within a few hours after hatching.

Numerous eggs of *Gobipteryx* and *Gobipipus* were collected from three egg-bearing localities of the southern Mongolian Gobi Desert by Polish-Mongolian and Soviet-Mongolian expeditions. Nesting sites in the Gobi Desert suggest that some enantiornithine birds laid eggs on the ground (Mikhailov 1996; Kurochkin et al. 2013). The eggs were small and oval, about 40 millimeters long and 20 millimeters wide, with slightly asymmetric two polar ends, with one end more pointed than the other. I have studied the sedimentary matrix of these Mongolian eggs that suggests that these eggs were buried in a noneolian environment, possibly in alluvial fan or braid-plain environments marginal to dune fields or within interdunal corridors. The eggs of Barun Goyot Formation were probably laid on the banks of ephemeral rivers and lakes. It is likely that these enantiornithine birds abounded in Cretaceous terrestrial ecosystems of the Gobi and lived in colonies, as evident from the distribution of eggs. The abundance of eggs of *Gobipipus* and *Gobipteryx*, occurring at different levels in the weathered slope of "Bird's Hill" at the Khermeen-Tsav locality of southern Gobi indicates that this area was a repetitive nesting site for these birds.

The taphonomic setting of the nesting site in the Gobi is interesting. Mikhailov (1992, 1996) interpreted these sites as long-term colonial nesting areas along the margins of lakes and estuaries. There was always a hazard of nesting at the water's edge because of occasional floods. The egg shape of *Gobipipus* and *Gobipteryx* is always preserved without any distortion, though the thin shell in some cases may be completely dissolved or destroyed. Separate eggs always exhibit a subvertical position and are evenly distributed within a layer of sandy matrix, close to each other; yet, these arrangements of eggs are random without any hint of forming a definite clutch. There are two interpretations of this unusual distribution of eggs. Like modern megapodes, *Gobipipus* and *Gobipteryx* might have laid separate eggs buried underground in mounds of sands and rotten vegetation, but lack of vegetation in the nesting site precludes this possibility. Alternatively, the eggs could have been primarily arranged in clutches, but as a result of frequent flooding of the nesting colonies, some of them were washed out from the nests and floated in vertical position (which is usual for avian eggs after some days of incubation). As the water level dropped, the eggs would slowly sink to the soft bottom substrate in a vertical position. Strong recrystallization of the eggshell, filling of pore canals with secondary calcite, and fusion of the eggshell surface all collectively favor the second scenario of recurrent flooding of nesting sites, a feature common among modern shorebirds (gulls, sterns, some waders, and ducks). Nests were perhaps open, with eggs laid on the ground, and were often flooded as a result of fluctuating water levels (Kurochkin et al. 2013).

Dyke et al. (2012) reported a drowned breeding colony of enantiornithines from the Late Cretaceous deposits of Romania. Apparently, these birds were aquatic foragers and laid eggs on sand bars and riverbanks, and the nesting sites were swamped by rising water. A lens of calcareous mudstone contains thousands of tightly packed eggshell fragments, seven near-complete eggs, and numerous embryonic and adult skeletons of enantiornithine birds. The colony must have been large, containing hundreds of nests. The form of the eggs and the ossified

skeletons of embryos indicate ground-nesting enantiornithines that produced precocial young. The absence of vegetation in the accumulation implies that the birds laid eggs in the depressions or scrapes in the sediments, as do plovers and some other waterside-nesting birds. Most likely, the thin egg-bearing mudstone layer captured a single flood event that drowned a large breeding colony of enantiornithine birds.

Slow Growth

Living altricial birds grow up rapidly within a year and start to fly near the completion of growth. However, enantiornithine birds had precocial development and would fly immediately after hatching. Bone histology has revealed that enantiornithines grew fast during early development, but experienced interruptions in their rate of bone generation during later growth. They reached a significant of fully body size by the initial fast-growing stage (Chinsamy-Turan 2005). The limb bone microstructure of enantiornithines shows several concentric lines of arrested growth like the growth rings of a tree that suggest that these birds did not reach full size within a year but needed several years to reach adulthood, as do some modern precocial birds. It is likely that the sluggish growth rate of enantiornithine birds was caused by the early onset of flight.

Flight Improvement

Enantiornithines underwent a dramatic reduction in body size from that of their pygostylian ancestors such as *Zhongornis*, *Sapeornis*, and *Confuciusornis*. The Early Cretaceous enantiornithines were small birds like modern passerines, ranging in size from that of a sparrow to that of a thrush. Smaller sizes reduced wing loading substantially in early enantiornithines (about one-fourth of contemporary *Confuciusornis*), which made them more maneuverable and less energetically expensive. Bird size may be the most important indicator of maneuverability because the gap between aerobic power available and minimum power required for steady flight increases (percentage wise) as size decreases. This gap is available for increased maneuverability. Little birds are more maneuverable because of the large margin of available power over power required for steady fight (see chapter 12). The smaller the bird, the better the flight performance. Other than size reduction, the streamlined body, short tail, modernization of flight apparatus, full range of wing excursion, and development of an additional winglet (the alula) suggest a great deal of flight improvement in enatiornithines from their pygostylian progenitors. With increased wingspan and muscle development, Enantiornithes developed ground takeoff ability, replacing the need for tree climbing.

Enantiornithines were strong fliers. They had developed fully powered flight with complex wing movements and strong flight muscles. The glenoid of the shoulder joint faces dorsoventrally, allowing a high-amplitude wingbeat during flapping flight. The wingbeat frequency was greatly enhanced by the supracoarcoideus pulley to enhance the upstroke by rapid rotation of the humerus, and a strut-like coracoid, which is clearly braced to the sternum to withstand the compressive force of the downstroke. The sternum became larger with the development of a short keel for the origin of the flight muscles. The V-shaped furcula is spring-like and could expand and contract during each wingbeat in concert with the aeration of the air sacs to absorb the shock, while the ventral hypocleidium added strength to the rib cage.

The wing elements were considerably modified from the basal pygostylian condition where the forelimb proportions fall within the range of extant birds. The ulna is longer than the humerus to generate powerful thrust during downstroke. It becomes stout and strong to support secondary feathers. The longer forearms and interlocking wrist bones with the metacarpals executed complex flight movement. Metacarpals II and III are fused to provide a strong platform for the attachment of primary feathers, while metacarpal I grew smaller and supported the alula. There is a digital reduction in the fingers, indicating that hands were no longer used for grasping. Unlike the flight apparatus, the hindlimb is still primitively designed. There is increased fusion in the foot bones and in the hips, so that the hindlimbs could function as landing gear.

Enantiornithines gained slow flight capability with the development of an alula, a short tuft of feathers attached to the first digit that creates a slot along the wing's leading edge that functions as a high-lift device similar to the leading edge slot of an aircraft. When a flying bird tilts its wings to slow its speed, air passing over the wing separates from the surface and breaks up into eddies, creating turbulence above the wing that can cause stalling. The alula breaks up boundary-layer turbulence and channels air over the wing surface so that the wing functions as the high angle of attack necessary for low-speed flight. By moving the thumb, enantiornithines could separate the feathers of the alula from the rest of the wing, creating a slot that helps low-speed, maneuverable flight necessary during takeoff and landing. Enantiornithines had the ability to fly slowly without stalling, a critical milestone for navigating through three-dimensional spaces such as flying through branches to land and perch. With the development of flapping flight and an alula, Enantiornithes could fly to the trees directly from the ground for perching without climbing tree trunks. Ground takeoff was a great improvement in the flight repertoire of enantiornithines. With the acquisition of flapping flight, a short pygostyle, large flight muscles, and an alula, enantiornithines became highly maneuverable, long-distance fliers. It seems that most avian flight-related advances were in place in enantiornithines except for the deeper sternal keel, stronger wing elements, a compact hand with fused carpometacarpus and loss of manual claws, a shorter back and tail, an enlarged and narrow synsacrum, and well-developed landing gear, which we encounter in *Ichthyornis*, a Cretaceous carinate from Kansas, as discussed in the following chapter.

Sexual Display

Elongate, steamer-like retrices have been reported in several enantiornithine taxa such as *Protopteryx*, *Paraprotopteryx*, *Dapingfangornis*, and *Bohaiornis*, which have little aerodynamic function but may have been used as display structures to attract and seduce a mate.

9 Ornithuromorphs: The Prelude to Modern Birds

Tell me, O Swan, your ancient story
From which country do you come?

Kabir, *Songs of Kabir*, a fifteenth-century Indian mystic

Predecessors of Modern Birds

The origin of modern birds from their Cretaceous ancestors is not fully understood because of the limited fossil record. Traditionally, two Cretaceous ornithurine birds from America's inland sea, ichthyornithiforms and hespeornithiforms, were generally regarded as the forerunners of modern birds that began to appear in the Early Tertiary period. In recent times, additional discoveries of nonornithurine Cretaceous birds fill major gaps in the evolutionary transformations. Enantiornithes and Ornithuromorpha represent two major radiations of Cretaceous birds. The evolutionary road that led to modern birds was represented by the ornithuromorphs, which include both ichthyornithiforms and hespeornithiforms along with several other basal taxa as well as all ten thousand species of living birds. Although enantiornithines were the dominant avialan clade during the Cretaceous, their sister clade Ornithuromorpha also made its debut during the Early Cretaceous time. Some ornithuromorphs continued throughout the Late Cretaceous and occupied a wide range of ecological niches. They are more closely related to the crown group Aves than are most of the other Cretaceous birds. They are critical to our understanding of the evolution of long-distance maneuvering flight and the emergence of the morphologies and unique physiology seen in all living birds.

Luis Chiappe (2002) defined the clade Ornithuromorpha as the common ancestor of *Patagopteryx* and Ornithurae plus all its descendants, characterized by the following derived characters: the caudal prezygapophyses are lost; the scapular blade is sagitally curved; metacarpals II and III are partially or completely fused distally; the intermetacarpal space is as wide as the maximum width of the shaft of metacarpal III; and metatarsals II, III, and IV are completely fused. The ornithuromorphs were lightly built and tended to be larger than their contemporaneous enantiornithines. Their skeletons and plumage show clear evidence of enhanced aerodynamic capabilities and improved terrestrial locomotion that distinctly differentiate them from their sister-taxon enantiornithines. They had become modernized in the structure of their flight apparatus, as revealed by a suite of derived characters, including powerful and elongated wing elements; the globose humeral head for a wide range of wing motion; the reduction and

fusion of metacarpals to form the avian carpometacarpus; interlocking wrist joints; digital reduction and loss of terminal claws; a shorter and stronger trunk with a rigid armature; a reduced and plowshare-shaped pygostyle with a fan of feathers; a well-developed sternum with a deep keel projecting anteriorly; a shoulder joint with an efficient supracoarcoideus pulley; a curved and distally tapering scapula; development of the lateral coracoid and sternocoracoidal processes; and the U-shaped furcula. In addition to the flight apparatus, there are several derived features in the pelvis and hindlimb morphology, including a narrow and enlarged synsacrum with increased sacral vertebrae; powerful hindlimbs with long and fused tarsometatarsuses; distally fused second and third metatarsals; and completely fused metatarsals II–IV with a primitive hypotarsus. The modification of the hip and hindlimb not only enhanced cursorial locomotion of ornithuromorphs, but also functioned as effective landing gear that could absorb impact forces. In addition to improved locomotor modules, there was modification of the temporal configuration of the skull with the loss of the postorbital bone, allowing streptostylic movement of the quadrate to power cranial kinesis. The brain was considerably enlarged, as revealed from endocasts, with typical avian architecture. In addition, the growth pattern as interpreted from the microstructure of the limb bones indicates fast growth like in modern birds. With the development of skeletal and neurological innovations and upgrading of the flight apparatus, ornithuromorphs were able to take long-distance flight across wide oceans and became globally distributed. With their skull configuration, enlarged brain, modern flight apparatus, powerful hindlimbs, and fast rates of body maturation, the ornithuromorphs show close evolutionary links to modern birds. However, basal ornithuromorphs retain some primitive features, such as teeth and lack of an ilioischiadic fenestra in the pelvis, which are absent in modern birds.

Radiation of Basal Ornithuromorphs

Unlike the explosive radiation of enantiornithines, Cretaceous Ornithuromorph fossils have remained rare,

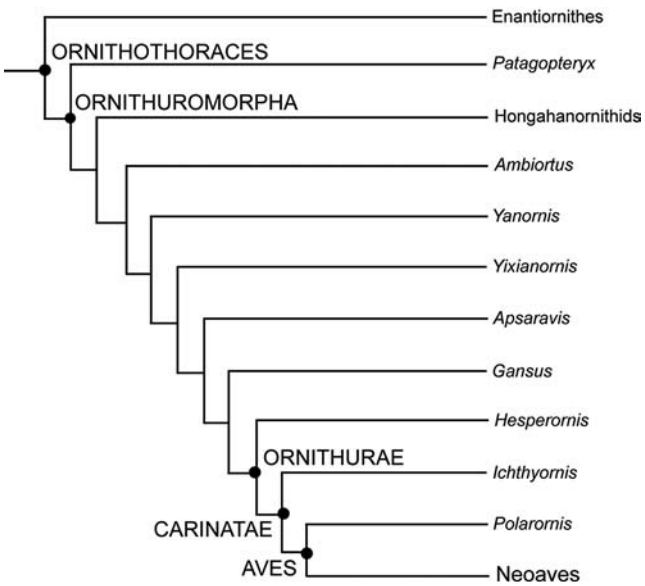


Figure 9.1. Phylogeny of ornithuromorph birds from Cretaceous deposits.

often represented by fragmentary remains, such as *Vorona* from Madagascar, *Ambiortus* from Mongolia, and the flightless bird *Patagopteryx* from Argentina that appear to be more derived than Enantiornithes, but less so than the Ornithurae. Basal ornithuromorphs, until recently, were one of the most poorly documented chapters in the early evolution of birds. In recent times, a series of non-ornithurine ornithuromorph fossils have been discovered from the Early Cretaceous Jehol deposits of China, including *Hongshanornis*, *Longicrusavis*, *Yanornis*, *Yixianornis*, *Songlingornis*, and *Gansus*, which have provided critical insights into the anatomy and early radiation of this clade. Other Late Cretaceous ornithuromorphs have been found in North America, Mongolia, and Antarctica. They show a wide variation in body size, ecological adaptations, flight improvements, and diet. The genealogical relationships of the early radiation of ornithuromorphs are shown in figure 9.1.

Patagopteryx from Patagonia

Herculano Alvarenga and José Bonaparte (1992) described a chicken-sized, flightless bird, *Patagopteryx deferrariisi*, from the Rio Colorado Formation of Patagonia (fig. 9.2). *Patagopteryx* was a small bird, about the size of a chicken.

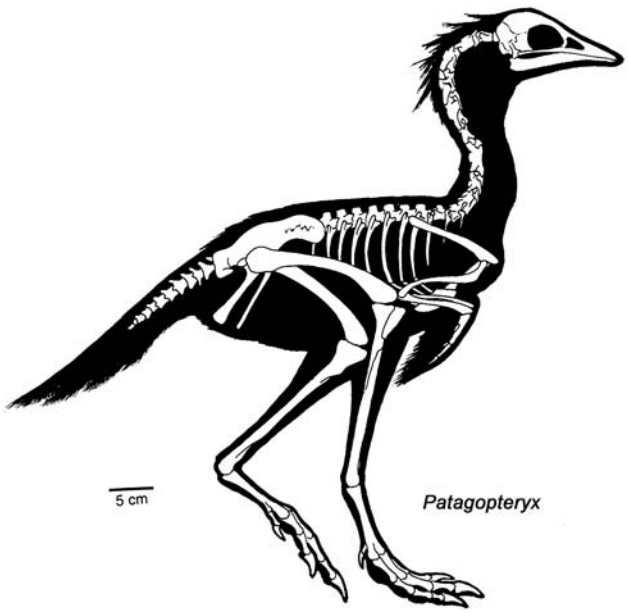


Figure 9.2. Reconstruction of the chicken-sized flightless bird *Patagopteryx deferrariisi* from the Late Cretaceous of Patagonia (after Chatterjee 1997).

The specimen was discovered accidentally from the campus grounds of the Comahoe National University during its expansion and renovation. *Patagopteryx* is known from several articulated specimens (Chiappe 1996). The skull is known only from the caudal part, showing a rounded braincase, a large orbit, and zygomatic and orbital processes. Most likely *Patagopteryx* retained teeth in its jaws like other early ornithuromorphs but modified the primitive diapsid configuration. The cervical and anterior dorsal vertebrae are heterocoelous and developed S-shaped necks like those of modern groundbirds. The wing is highly atrophied, a sign of secondary flightlessness. The humerus is reduced but retains a bicipital crest. The shoulder girdle is incomplete; the coracoid shows a depression on the posterior surface, as seen in enantiornithine birds. The clavicles are fragmentary. The pelvis and hindlimb are well preserved. The ilia form a pelvic shield with the synsacrum; the latter is dorsoventrally compressed and transversely wide. The pelvis is opisthopubic and resembles that of ratites, where the ischium and pubis are slender rods; the ilium and ischium separate posteriorly without enclosing the ilioischiadic fenestra. The pelvis is very wide with the loss of the puboischiadic symphysis, indicating that the pelvic canal became large for laying bigger eggs. A large antitrochanter is present on the rim of the acetabulum. The hindlimb is well developed, as in all flightless birds. The femur is robust and shows a prominent popliteal space. The tibiotarsus has a lateral cnemial crest. The distal tarsals and metatarsals are fused to form the tarsometatarsus, and the latter develops a tendinal groove distally without a supratendinal bridge. All these pelvic specializations indicate that *Patagopteryx* was a terrestrial walker and may represent the most basal radiation of ornithuromorphs.

The short wings, simplified pectoral girdle, loss of a wishbone, and massive legs are clearly related to the flightless nature of *Patagopteryx*, indicating that avian flight was lost at every major stage of avian evolution. As Paul (2002) has suggested, there are two modes of radiation of Mesozoic birds: one led to the conquest of the air with the refinement of the flight apparatus, and the other in the opposite direction with flightlessness that transformed aerial birds back into groundbirds with atrophied wings and powerful hindlimbs. Thus the evolution of flight in birds is not a linear improvement, but often took U-turns that erased all the past history of upgrading the flight apparatus, but left critical signs of evolutionary transformations in nonflight skeletons. The interplay of two opposing forces in bird evolution, improvement of flight and loss of flight, operated throughout the history of bird evolution, often associated with the development and loss of cranial kinesis.

Ornithuromorphs from China

In recent decades, a variety of ornithuromorph birds have been discovered from the Early Cretaceous Jehol group of China, including *Archaeorhynchus*, *Hongshanornis*, *Longicrusavis*, *Yanornis*, *Yixianornis*, *Songlingornis*, and *Gansus*, which are represented by complete and well-preserved skeletons, often with intact plumages and fan-shaped tails that provide critical information on the basal anatomy of the clade with a mosaic of primitive and advanced characters. These Chinese ornithuromorphs were primitive in the configuration of the pelvis, charac-

terized by a narrow pelvic canal, where both the ischium and pubis retained a ventral symphysis that indicates early stages of ornithuromorph radiation. Some of these Chinese ornithuromorph taxa are described below.

Hongshanornithidae

Two closely related archaic species of ornithuromorphs, *Hongshanornis longicresta* (Zhou and Zhang 2005) and *Longicrusavis houi* (O'Connor et al. 2010), are known from the Early Cretaceous Yixian Formation in Inner Mongolia and Liaoning Province, respectively, and are included in the family Hongshanornithidae. They were small, about the size of modern plovers, with strong flying ability. Their legs are proportionately long in comparison to the wings, suggesting they were probably aquatic wading birds, foraging in shallow waters in search of small fish, crustaceans, and other invertebrates. Lake environments probably played a key role in the lifestyle of these wading birds, unlike that of other arboreal Jehol birds. They had reduced teeth in the jaws and developed a predentary bone in front of the mandible.

Hongshanornis had a pointed beak possibly with few teeth at the tip, a distinctive head crest of plumage for display, a triangular antorbital fenestra, a large orbit, and an expanded braincase (fig. 9.3A). The jugal bar is slender, rod-shaped, and lacking any ascending process, and was probably mobile for cranial kinesis. The dentary is more than half the length of the lower jaw and has a distinctive sigmoidal mandibular rami such that the dorsal margin of each ramus is rostrally convex and caudally concave. At the tip of the dentary, there is an interdental bone (intersymphysial ossification) to strengthen the symphysis of the jaws. The neck is moderately long but the anteriormost vertebrae appear to be heterocoelous. The thoracic ribs are strengthened by an uncinate process, but slender gastralia are still retained. The synsacrum is large and fused, followed by a short pygostyle. The scapula is long with a short acromion process, and the glenoid facet facing outward and upward permitted rapid wingbeats. In addition, the coracoid is strut-like with a well-developed procoracoid process, indicating the development of a supracoracoideus pulley for the upstroke. The furcula is U-shaped with a short hypocleidium. The sternum is longer than wide with two pairs of posterior excavations but lacks the ventral keel. The proportions of wing elements are primitive, with the humerus longer than the ulna and the manus longer than the humerus. The humerus is robust with a prominent spherical head and a large deltopectoral crest. The carpometacarpus is well fused proximally with a well-developed trochlear surface. The manus retains the claws in the second and third digits. Digit 2 is the robust and the longest in the series; the phalangeal formula is 2-3-2-x-x. The pelvic bones are articulated; the pubis is slender and retroverted and lacks the distal foot. The leg bones are much longer and more slender than the wing elements; the fibula is atrophied

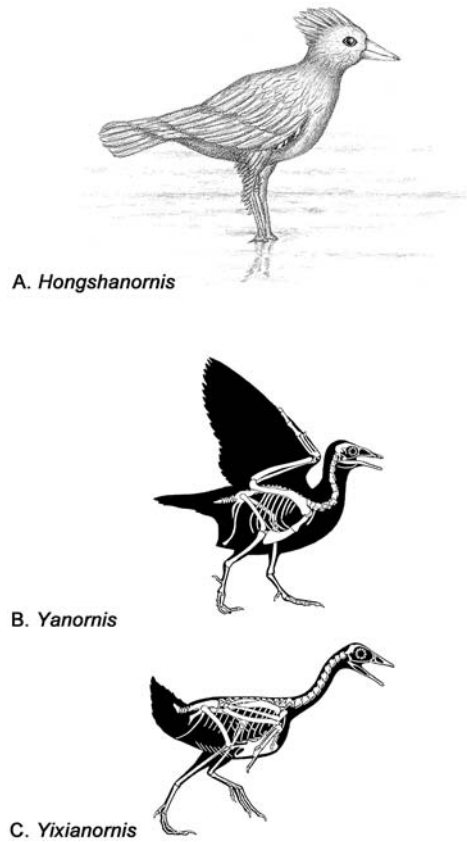


Figure 9.3. Some ornithuromorph birds from the Early Cretaceous of China. A, life restoration of *Hongshanornis longicresta*, a plover-sized wading bird. B, skeletal reconstruction of *Yanornis martini*, a shorebird that lived along the lake margin (Zhou and Zhang 2001). C, skeletal reconstruction of *Yixianornis grabaui* (Zhou and Zhang 2001).

considerably and fails to reach the distal end of the tibiotarsus. The tarsometatarsus is completely fused. The fifth metatarsal is completely absent, and the three major metatarsals (II–IV) are nearly the same width. The feathers are beautifully preserved in the wings in association with the skeleton, with long and asymmetric flight feathers and an alula.

Like the closely related genus *Hongshanornis*, *Longicrusavis* was a small, phoebe-sized bird and is represented by a nearly complete skeleton. These two Chinese ornithuromorphs share an unusual sigmoid mandible and elongated hindlimbs relative to their forelimbs as in wading birds. Although these two taxa are similar in size and morphology, there are some unique characteristics in *Longicrusavis*, such as lack of a strong constriction at the base of the relatively long and robust rostrum, absence of a medial sternal process, and the presence of a supracondylar process on the humerus. Several specializations of the hindlimbs such as an elongate tibiotarsus with proximally projecting cnemial crests, elongate proximal phalanges, and a short hallux suggest that hongshanornithids were wading birds that foraged on aquatic food.

Yanonornis

Yanonornis martini from the Early Cretaceous Jiufotang Formation was a chicken-sized ornithuromorph with a long skull studded with numerous teeth, ten teeth in the upper jaw and twenty teeth in the lower jaw (Zhou and Zhang 2001). It was an opportunistic feeder, as the remains of fish in the stomach contents as well gastroliths suggest a diet-switching habit (Zhou et al. 2004). The dentary is shorter than the skull, about two-thirds of its length. The nasal opening is slender and large, followed by a reduced antorbital opening and a large and circular orbit. The frontoparietal region is expanded to house a large brain. The jugal forms a slender bar and the quadrate is streptostylic with the development of an orbital process. The skull is modified from the primitive diapsid condition with the reduced postorbital bar and perhaps developed a primitive form of cranial kinesis (fig. 9.3B).

In the postcranial skeleton, the cervicals are heterocoelous, whereas the dorsal vertebrae are elongate and contain deep pleurocoels. The synsacrum is enlarged, containing nine fused vertebrate. The pygostyle is highly abbreviated. The shoulder girdle is modernized like that of modern birds with the development of a flat and curved scapular blade with a large acromion process, a strut-like coracoid with procoracoid and acrocoracoid processes, and a cotyle for scapular articulation. The furcula is U-shaped and compressed anteroposteriorly. The sternum is long with a well-developed keel extending along its full length and contains a pair of elliptical fenestrae posteriorly. The forelimb is longer and more powerful than the hindlimb, with the ulna longer than the humerus and the manus. The deltopectoral crest of the humerus is well developed with a spherical head and a prominent ball-shaped bicipital crest. The ulna has a semicircular dorsal condyle at the distal end for flexion and extension of the hand. The carpometacarpus is fused at both ends but the claws are retained in the first two digits. The ilium is expanded mediolaterally and extended considerably anteriorly and is probably fused with the sacrum to form the synsacrum. The pubis is slender and curved backward. The ischium is shorter and tapers distally. The femur is bow-shaped and considerably shorter than the tibiotarsus, indicating adaptation for wading. The tarsometatarsus is completely fused and elongated. Metatarsal I is reversed and articulates with metatarsal II distally. The unguals are relatively short.

Most likely, *Yanornis* was a shorebird along the lakes of the Jehol environment foraging on fish, as the stomach contents imply. It has been suggested that it occasionally switched to seeds, as gastroliths in the stomach indicate, which are usually linked to an herbivorous diet (Zhou et al. 2004). However, this interpretation may not be correct because modern loons often swallow pebbles from the bottom of the lakes that help digestion of their food and act as a ballast. These gastroliths assist the loon's gizzards in crushing hard parts of the loon's food, such as crustaceans and the bones of fish and other small vertebrates. *Yanornis* probably adapted similar use of gastroliths for grinding skulls and bones of fish.

Yixianornis

Yixianornis grabaui is found along with *Yanornis* in the Early Cretaceous Jiufotang Formation of China known

from a nearly complete skeleton surrounded by clear impressions of the wing and tail feathers (Zhou and Zhang 2001; Clarke et al. 2006). In size and many anatomical details, *Yixianornis* is very similar to its close relative *Yanornis*, at about the size of a chicken, but somewhat more advanced in the development of a large and highly keeled sternum (fig. 9.3C). The skull of *Yixianornis* is ventrally exposed, showing a large orbit surrounded by sclerotic rings, and had an expanded frontal to accommodate a large cerebellum. Sclerotic rings are generally associated with a diurnal lifestyle in modern reptiles and birds. The jugal bar is slender and rod-like and lacks an ascending process, indicating some propalinal motion during kinesis. The dentary is about half the length of the skull. The teeth are present at the tips of the premaxilla and the dentary in distinct sockets. The tooth crown is unserrated with peg-like morphology. The mandible is narrow anteriorly and quite thin and delicate.

There are about ten heterocoelous cervicals and more than ten thoracic vertebrae with lateral excavations on the centra, nine sacrals, and five free caudals. Four caudal vertebrae have contributed to the formation of a plowshare-shaped pygostyle that supported fanlike tail feathers as seen in modern birds, providing a large lifting surface. About fifteen delicate gastralia are retained primitively in this bird. The coracoid is strut-like and modern looking with development of both procoracoid and acrocoracoid processes and a deep cotyle for the scapula. The scapula is as long as the humerus; its blade is recurved and tapers posteriorly. The acromion extends anterior to the pronounced hemispherical coracoid tubercle. The sternum is enlarged with a well-projected keel and contains a distinct opening posteriorly on each side. The humerus is as long as the ulna with a globose head with a large deltopectoral crest. The ulna has semilunate trochlear surface for sliding the carpal bones. The metacarpals are fused with distal carpal bones to form a carpometacarpus, but the claws are retained in the hand. The hips and hindlimbs show more primitive features than the forelimbs as in early ornithuromorph birds. The pelvic bones are fused with elongated preiliac and postiliac processes. The pubis is very long and rod-like, directed backward. The ischium is much shorter than the pubis and broad, but tapers distally. The femur is somewhat bowed; it is shorter than the tibiotarsus, but longer than the tarsometatarsus. The phalanges are delicate and support highly recurved claws.

Gansus

Gansus yumensesis, a foot-propelled diving bird from the Early Cretaceous Xiagou Formation (105 to 115 million years ago) of the Changma Basin of Gansu Province of northwestern China, is known from several excellent, three-dimensional skeletons associated with soft tissues, such as flight feathers, skin, and traces of webbing between their toes (You et al. 2006). The fossils were found some 2,000 kilometers west of Jehol Group localities in lacustrine mudstone facies. In these lake deposits, *Gansus* appears to be the most common bird, representing about 80% of the bird fossils that have been discovered at this site, but none include the bird's skull. Apparently, there was some postmortem separation of the head from the rest of the body. *Gansus* was about the size of a tern. Recent study has identified melanin, the color pigment of feathers, in *Gansus*. The anatomy of *Gansus* indicates specializations for an amphibious lifestyle. The powerful wings, the cranially projecting bicipital crest on the humerus, the fused carpometacarpus, the reduced alular digit, the U-shaped furcula, the large sickle-shaped keel on the sternum, the strut-like coracoid with a supracoracoideus pulley, and asymmetric flight feathers clearly indicate that *Gansus* was an acrobatic flier. On the other hand, the hindlimbs show several foot-propelled diving adaptations as seen in the Late Cretaceous *Hesperornis* as well as modern loons, grebes, and diving ducks. These features include a large and elongate proximocranially projecting cnemial crest on the tibiotarsus, the proximal position of the trochlea of metatarsal II, webbed feet, and a highly reduced pygostyle. The relative length proportions of forelimbs and hindlimbs of *Gansus* show measurements similar to those of living ducks and foot-propelled divers such as loons and grebes, suggesting similar habitats. Unlike *Hesperornis*, *Gansus* was both volant and capable of diving to some degree using either its feet or, perhaps, both its wings and its feet for underwater locomotion. *Gansus* is one of the most advanced

nonornithurine birds known and is a sister taxon of the more derived clade Ornithurae.

Ornithuromorphs from Mongolia

Two ornithuromorph bird fossils are known from the Cretaceous of Mongolia, a primitive *Ambiortus* from the Early Cretaceous and a more derived *Apsaravis* from the Late Cretaceous deposits.

Ambiortus

Evgeny Kurochkin (1985) described a partial associated skeleton of a crow-sized bird, *Ambiortus dementjevi*, along with feather impressions from the lacustrine deposits of Mongolia. The material consists of the left pectoral girdle and wing, including the scapula, the coracoid, the proximal half of the humerus, the carpometacarpus, a partial sternum and furcula, and a series of thirteen presacral vertebrae. Unfortunately, like most other Early Cretaceous birds, the skull of *Ambiortus* is unknown. *Ambiortus* shows a refined level of flight capability, as seen in *Ichthyornis*. It has a keel on the anterior part of the sternum, a strut-like coracoid with a triosseal canal, a wide and spatulate sternal end of the coracoid, a U-shaped furcula, a humerus with a well-developed crest, a deltopectoral crest, and a carpometacarpus.

I had the opportunity to study the holotype of *Ambiortus dementjevi* (fig. 9.4A). Like other Cretaceous birds, *Ambiortus* displays a mosaic of primitive and advanced features. The lack of a bicipital crest on the humerus, the amphicoelous centra, the wide clavicular angle of the furcula, and the retention of the third phalanx in the second digit of the wing are some of the primitive characters.

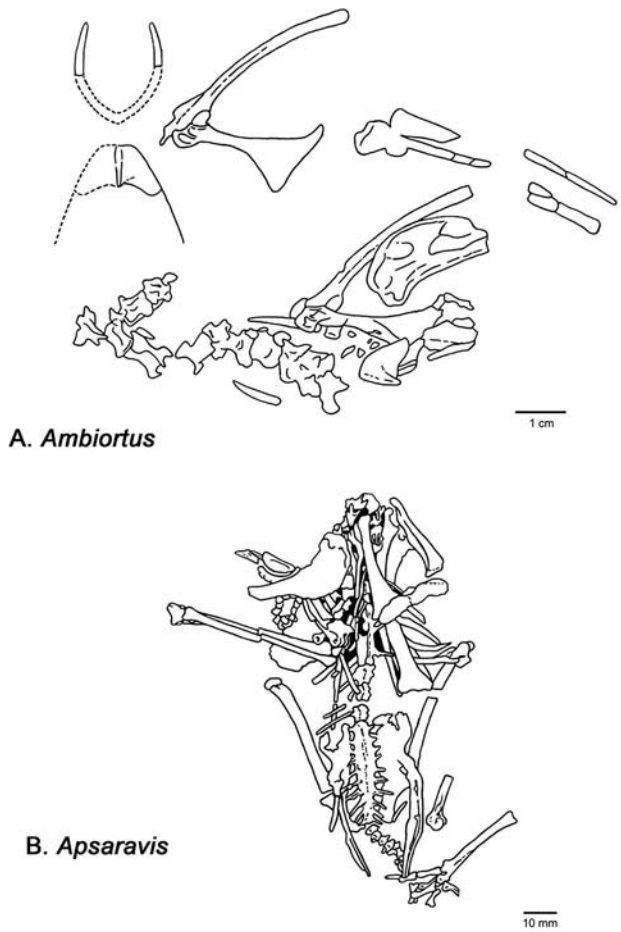


Figure 9.4. Ornithuromorph birds from the Cretaceous of Mongolia. A, skeleton of *Ambiortus dementjevi* from the Early Cretaceous of Mongolia as found; inset, restorations of furcula, anterior view; and scapulocoracoid, left lateral view; drawn from the original holotype specimen (after Chatterjee 1999). B, skeleton of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia as preserved (after Clarke and Norell 2002).

Apsaravis

Apsaravis ukhaana, a highly derived ornithuromorph bird from the Late Cretaceous Djadokhta Formation of the southern Mongolia, is known from a beautiful skeleton (Clarke and Norell 2002). It was a medium-sized bird, about the size of a mallard, with a toothless beak, powerful wings, and a foot with only three toes (fig. 9.4B). The skeleton shows several features of modern birds, including a fused jaw symphysis, heterocoelous cervicals, a reduced thorax, and a broad pelvis. The pubis and ischium are well separated distally and the loss of a symphysis is probably linked to the evolution of a wide pelvic canal for laying larger eggs. The hand is modern looking with the development of an extensor process, a bony projection on metacarpal I for the attachment of the propatagial ligament that helps unfolding of the wing automatically during the downstroke. This strong ligament supports the propatagium, or the forewing, a flap of skin between the wrist and the shoulder that can change the camber of the wing especially during takeoff and landing like the

flap of an aircraft, indicating further refinement of flight in this lineage.

Paleoecology of Basal Ornithuromorphs

Basal ornithuromorphs exploited a wide range of feeding habits and lifestyles. The flightless *Patagopteryx* in Argentina was fully terrestrial and probably fed on small animals from the ground or flying insects. Many of the Chinese ornithuromorphs such as *Yanornis* and *Yixianornis* were probably waterbirds, congregated around the Jehol lakes, and exploited aquatic food with their elongated jaws equipped with sharp teeth. Some of these birds such as hongshanornithids became waders like plovers as suggested by their pointed beak and long lower legs, foraging in shallow waters in search of small fish, crustaceans, and aquatic prey; others such as *Gansus* became volant diving birds like modern loons, grebes, and ducks as suggested by their by powerful legs and webbed feet. Some of these aquatic birds such as *Yanornis* probably used gastroliths in crushing the hard parts of the aquatic food such as exoskeletons of crustaceans and bones of fish like modern loons. Apparently there was a niche partitioning among Jehol birds in the Early Cretaceous time, showing behavioral plasticity in food choice that increased resource exploitation in communities with more species. Early avialans, pygostylians, and enantiornithines in the Jehol environment preferred trees for feeding on insects and seeds, whereas early ornithuromorphs became largely waterbirds, gathering along lakefronts to forage for fish and other aquatic invertebrates. Some became skilled swimmers and divers. Perhaps these aquatic adaptations of early ornithuromorphs led to more specialized Late Cretaceous marine ornithurine birds such as *Hesperornis*, *Parahesperornis*, *Ichthyornis*, and *Baptornis* that thrived in the Western Interior Seaway of North America. Highly volant Mongolian ornithuromorphs such as *Asparavis* with their edentulous beaks probably exploited high-fiber food items such as seeds and grains in the interfluves during foraging.

From an enantiornithine bauplan, early ornithuromorphs exhibit several improvements in maneuvering flight with fast wingbeats as seen in modern birds. These include a deep keel on the sternum for housing large flight muscles; a modern supracoracoideus pulley with the development of an acrocoracoid process, enabling high-amplitude upstroke; a globose humeral head, permitting complex wing motion; a pronounced extensor process on metacarpal I for automatic extension of the hand during downstroke; the development of a propatagium for changing the camber of the wing; and a short plowshare-shaped pygostyle with fan-shaped retrices that increased lift and allowed for complex maneuvers. Leg feathers were possibly lost in ornithuromorphs with the development of a monoplane wing planform that had already possessed a powerful lifting surface provided by the combined wing feathers and the tail feathers as in modern birds (see chapter 12). However, compared to the improved forelimbs, the hindlimbs and hip girdles retain many primitive features. The development of wide hips and the loss of puboischiadic symphysis in Late Cretaceous ornithuromorphs indicate improvement of reproductive strategy with the development of a wide pelvic canal for laying larger eggs.

Interrelationships of Ornithurae

Within Ornithuromorpha, Ornithurae form a derived clade that includes the Late Cretaceous marine birds such as hesperornithines and ichthyornithines as well as all modern birds (Aves). The interrelationships of higher taxa within Ornithurae are very controversial because some of the clades were introduced in the nineteenth century, when only a handful of Mesozoic birds were known. Various names have been used for different clades by different authors, a situation that violates the fundamental nomenclatural principle and stability.

Gauthier and de Queiroz (2001) recognized three major clades within Ornithuromorpha—Ornithurae, Carinatae, and Aves—to minimize ambiguity as we move up the cladogram of birds; the clade Aves includes all modern birds, the crown clade dinosaurs. I concur with this classification and these interrelationships and use the names of these three clades.

Ernst Haeckel coined the name Ornithurae in 1896 and included all "true birds" and their fossil relatives with

the characteristic abbreviated tail morphology of modern birds. In this sense, the Ornithurae includes Hesperornithes, Ichthyornithes, and modern birds. They share an avidiapsid temporal configuration where the orbit becomes confluent with two temporal openings with the breakdown of diapsid arches, thus permitting cranial kinesis.

After Ornithurae, the next step on the cladogram of birds is marked by the clade Carinatae. The name Carinatae was proposed by Merrem in 1813 to include Ichthyornithes and modern birds with a keeled sternum. In this arrangement, Carinatae include two sister taxa, Ichthyornithes and Aves, a clade accepted by most recent workers.

The main taxonomic conundrum in ornithurine lineage is the alternate usage of the names Neornithes and Aves to designate the modern birds. Gadow proposed the name Neornithes in 1892 to accommodate both living and fossil groups of ornithurines such as Hesperornithes, Ichthyornithes, and modern birds, whereas Linnaeus erected the clade Aves in 1758 to include living birds. No doubt the name Aves Linnaeus 1758 has a nomenclatural priority over Neornithes Gadow 1892 for grouping modern birds. Moreover, Gauthier and de Queiroz (2001) pointed out that the name Neornithes was originally proposed to include fossil hesperornithines and ichthyornithines and living birds, an explicit substitute for Haeckel's Ornithurae and thus a junior synonym of Ornithurae; they recommended rejecting its usage. However, the nomenclatural problem was not resolved because different authors continue to use either Neornithes or Aves to include modern birds, depending on one's taste in terminology, as if they are interchangeable.

In this discussion the name Aves is used here to include modern birds containing about ten thousand living species (see chapter 11). Gauthier and de Queiroz (2001) defined Aves as the crown clade of birds stemming from the most recent common ancestor of flightless ratites and neognathous birds. In this book "avian" refers to crown clade birds as defined above. Several synapomorphies define Aves, including the absence of teeth; quadrate articulates with prootics; the presence of three articular facets on the ventral end of the quadrate; fusion of the symphysis between the two halves of the dentaries; the absence of gastralia; a pneumatic fossa and a foramen in the humerus; and a complex hypotarsus. Nested within the ornithuromorph radiation we see the emergence of basal lineages of modern birds in the Late Cretaceous ecosystem that would flourish and diversify explosively in the Cenozoic world soon after the KT extinction.

Ornithurae: Cretaceous Toothed Birds from Kansas

During the Late Cretaceous, between 84 and 65 million years ago, the continents continued to separate and began to assume their present-day positions. Great warm seas covered much of the Earth during this period, a time of mild climate and ice-free polar regions. Shallow seas from the Arctic Ocean flooded vast areas of North America, splitting the continents into two landmasses, Laramidia to the west and Appalachia to the east (fig. 9.5). This epicontinental sea, the Western Interior Seaway, almost 1,500 kilometers wide, at times stretched from central Utah to the western Appalachians and from the Arctic Ocean to the Gulf of Mexico. At times of low sediment supply and maximum lateral expansion of the seaway, chalks were laid down in the center of the basin. The most famous of these deposits is the Niobrara Chalk, which occupies the middle of a transgressive-regressive cycle. The Niobrara Chalk has yielded beautifully preserved vertebrate fossils, including ammonites, rudists, fish, turtles, plesiosaurs, mosasaurs, pterosaurs, and the basal ornithurine birds such as hesperornitheans and ichthyornithiforms. These ornithurine birds invaded seas for the first time in avian history; hesperornithines became successful divers, while ichthyornithines became sophisticated fliers over the large expanse of seawater. The Ornithurae show the following derived traits: a narrow, tapering orbital process on the medial side of the quadrate; fewer than eleven thoracic vertebrae; a procoracoid process on the coracoid; a globe-shaped proximal process on the humerus; a smaller acetabulum; a pubis running back parallel to the ischium and ilium; and a femur with a prominent patellar groove.

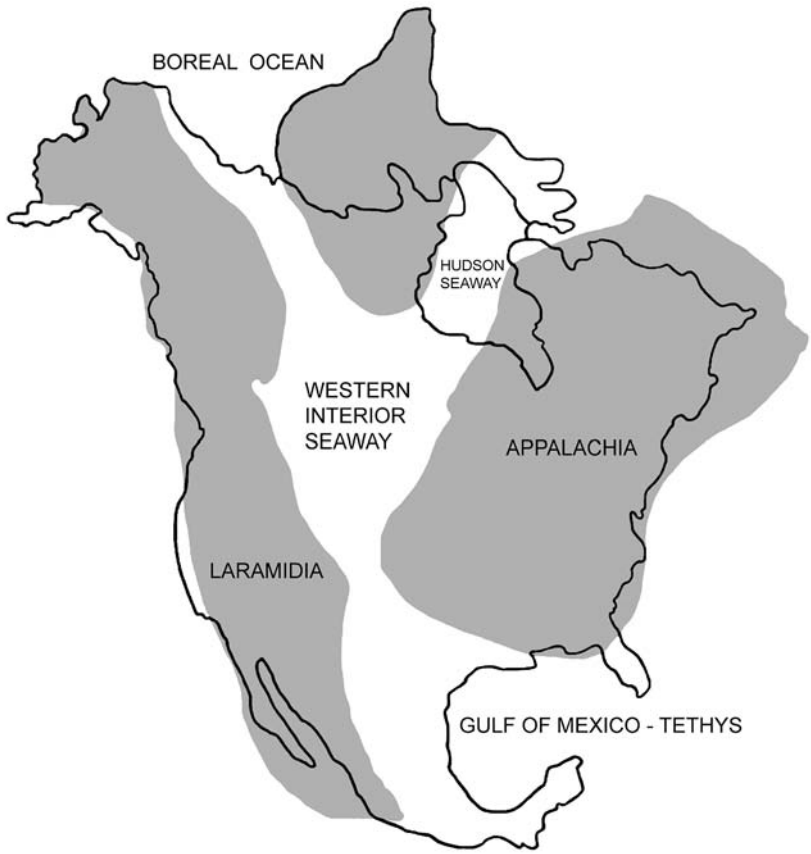


Figure 9.5. Western Interior Seaway during the Late Cretaceous period (about 75 million years ago), which was home to the marine ornithurine birds such as Hesperornithiformes and Ichthyornithes.

In 1880, when Othniel Charles Marsh published his magisterial book on Odontornithes, the Cretaceous toothed birds from the Niobrara Chalk of Kansas, it became an instant favorite among evolutionary biologists. The acceptance of these fossils as true birds was universal. Marsh's monograph is the most detailed description, bone by bone, of five species of toothed birds: *Hesperornis regalis*, *H. crassipes*, *Ichthyornis dispar*, *I. victor*, and *Apatornis celer*. The text is accompanied by excellent drawings of the individual bones and skeletal restorations. This book still ranks as one of the outstanding contributions to avian paleontology. These toothed birds from Kansas represented a triumph for Darwin. Darwin did not cite *Archaeopteryx* as a long-sought evolutionary intermediate to bolster his theory. He wrote to Marsh on August 31, 1880: "Your work on these old birds . . . has afforded the best support to the theory of evolution, which has appeared in the last 20 years [i.e., since the publishing of the *On the Origin of Species*]" (Yale Peabody museum archive n.d.).

Hesperornithes: Divers of the Cretaceous Seas

The Late Cretaceous hesperornithine birds in the Western Interior Seaway of North America further refined the diving adaptation pioneered by the Early Cretaceous *Gansus* in the Chinese lake environments. Hesperornithes represents a clade of foot-propelled diving birds parallel to modern loons and grebes in many skeletal features. However, they became so specialized in diving in the Cretaceous seas that they became secondarily flightless. The body was somewhat elongated and streamlined; the jaws were long; the feet were adapted for paddling; and the wings were suppressed, formed only by the splint-like humeri. The rest of the wing was lost. They followed the general trend of losing flight like other lineages of

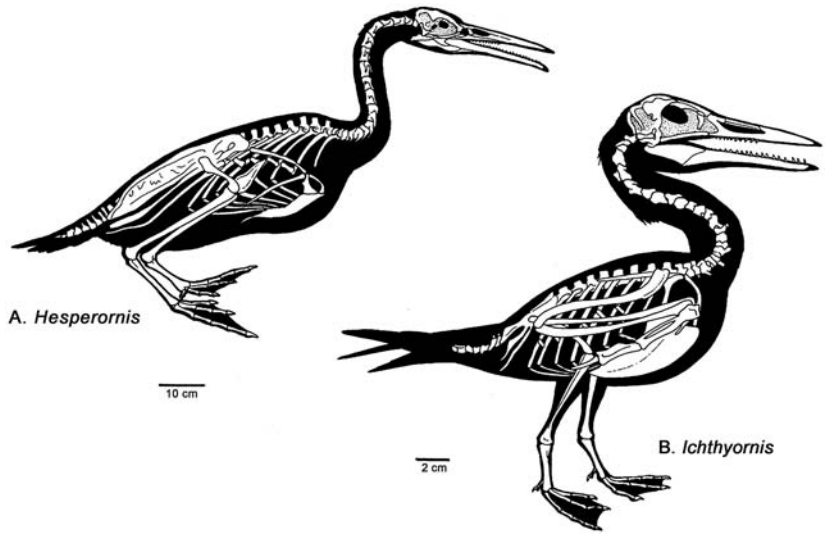


Figure 9.6. Late Cretaceous ornithurine birds from the Niobrara Chalk of Kansas. A, skeletal restoration of the foot-propelled diver *Hesperornis regalis*. B, skeletal restoration of the highly volant bird *Ichthyornis dispar* (after Chatterjee 1997).

birds, as they became highly aquatic divers. These birds are distinct from modern divers because they have true teeth in their jaws. The hesperornithines are the best-known Mesozoic ornithurine birds and show evidence of great diversity and cosmopolitan distribution during the Cretaceous; their fossils have been found in North America, Europe, and Asia. Although hesperornithine fossils are largely restricted to marine strata, some fossils have been found in continental and estuarine deposits. The earliest documented record of the hesperornithines is *Enaliornis* from the Lower Cretaceous of England.

The Niobrara Chalk and Pierre Shale Formations of Kansas, South Dakota, and Wyoming have produced three genera: *Baptornis*, *Parahesperornis*, and *Hesperornis*. The skull of *Baptornis* is poorly known, but the postcranial material is well represented. *Baptornis* was a less specialized diving bird than its contemporary, *Hesperornis*. Although these hesperornithines are flightless, early forms such as *Enaliornis* from England and *Pasquiaornis* from Canada hint at rudimentary flying capabilities, thus indicating that flightless hesperornithines evolved from flying ancestors. Flightlessness is a recurrent theme in every major lineage of avian evolution.

Larry Martin (1984) described an almost complete skeleton of *Parahesperornis alexi.* Although the skull of *Parahesperornis* closely resembles that of *Hesperornis*, there are certain differences between these two taxa in the morphology of the lacrimal and quadrate bones, the frontoparietal suture, the tympanic recess, and the braincase. The presence of soft, hair-like plumaceous feathers indicates that in life these birds had a furry look.

Hesperornis is by far the best-known genus in this group and has been studied by many workers since Marsh. It was a large bird, about 2 meters long and 1 meter tall, and has a long neck, reduced tail, and powerful legs (fig. 9.6A). The skull is about 26 centimeters long, with an elongate beak presumably covered by a horny sheath. The top part of the bill overhangs the lower part. The external naris is holorhinal and posteriorly set. Teeth are retained in a groove (instead of sockets) in the maxilla and the dentary but are absent from the premaxilla. Sutures are present in the dermal bones. The premaxillae are elongate and contact the frontal bones, and the upper jaw has been moved prokinetically (Witmer and Martin 1987). The temporal configuration is like that of modern birds in that the orbit is confluent with the two temporal openings. A deep recess borders the upper temporal opening. The postorbital and ectopterygoid bones are lost. The braincase is inflated and intimately fused with the skull roof. The quadrate is modern looking, with a

prominent orbital process. The dorsal head is single but expanded transversely so that it articulates with both the squamosal and the prootic. The two halves of the dentary are separate but connected to a small predentary bone. Along the roof of the orbits, there are well-marked depressions for salt glands, indicative of the aquatic habits of *Hesperornis*.

The postcranial skeleton was highly modified for foot-propelled diving habits and shows the evidence of flightlessness. The vertebrae are heterocoelous. The shoulder girdle is relatively primitive with an *Archaeopteryx*-like coracoid. It supported only a degenerate limb, the relic of a wing, the forearm and hand being lost. The sternum is flat and lacks a keel, and the furcula is not fused. The shoulder girdle and diminutive wings clearly indicate that *Hesperornis* could not fly. The pelvis and hindlimbs are typical of a foot-propelled diving bird, with relatively short, powerful legs placed far back on the body. The pelvis is narrow and compressed and the feet are located at the back of the body. The postacetabular process of the ilium is much more elongated than the preacetabular blade. The pubis and ischium are horizontal and extend posteriorly at the level of the ilium. The ilium and ischium remain separate throughout their lengths, without any fusion. The acetabulum is partially closed internally by a bone, and there is a prominent antitrochanter. The femur is extremely short and stout, directed horizontally in a lateral direction to position the foot.

A special feature in a foot-propelled diving bird is the development of a large cnemial crest on the tibia; the extensive muscles necessary for the power strokes used in diving attach to this crest. The way in which the cnemial crest is developed among different diving birds may be an important phylogenetic character. In *Hesperornis*, the cnemial crest evolved from the development and expansion of the patella. In grebes, on the other hand, both the patella and the tibiotarsus contribute to the formation of the cnemial crest. The cnemial crest of loons is derived solely from the tibiotarsus, and the patella has been reduced to a tiny remnant of bone. The tarsometatarsus is transversely compressed, and the fourth toe is the longest. The foot skeleton is similar to that of grebes and probably had lobed toes to increase the surface area for swimming and diving. In life, the femur and tibiotarsus would be enclosed by muscle and skin within the contour of the body and remained largely immobile; the principal swimming movement was at the ankles, where the feet paddled for locomotion. The toes were long and could spread widely. These foot-propelled divers had streamlined bodies and swam rapidly by kicking their feet. The dense, compact, and nonpneumatic nature of the limb bones may have been a specialization for increasing their weight for more effective diving. These birds foraged for fish along the coastlines of shallow seaways and returned to land only to reproduce. They must have been highly awkward on land because of the backward position of their legs and, apart from nesting, spent most of their lives in the water. These birds probably nested in rookeries on beaches or offshore islands as some juvenile specimens indicate. They used their long and toothed jaws for stabbing and capturing fish. The presence of cranial kinesis and mandibular spreading would facilitate gulping very large prey. A *Baptornis* skeleton associated with coprolites containing bones of small marine fish provides direct evidence for their piscivorous adaptation. They died out at the end of the Cretaceous along with enantiornithines.

Basal Carinatae: Ichthyornithes

Continuing up the cladogram of Ornithurae, we come to the immediate relatives of modern birds, Ichthyornithes, which is united with modern birds in the clade Carinatae. Merrem's (1813) original name Carinatae referred to the presence of a prominent keel, or carina, on the sternum in this group of birds, which is linked to the development of large flight muscles. With the discovery of a myriad of ornithuromorph birds in recent decades that show various stages of keel development, as well as loss of the keel in flightless birds, we need unambiguous characters to define Carinatae other than a keeled sternum. Some of the derived characters for this clade include a well-developed extensor process on the alular digit and loss of an ungual phalanx in the manual major digit (finger 2). Carinate birds are advanced in the structure of their

skull, wings, shoulder girdle, and sternum. Carinatae is used for the most recent common ancestor of Ichthyornithes and modern birds plus all its descendants.

Marsh (1880) described two volant, toothed birds from Kansas, *Ichthyornis* and *Apatornis*; these birds were smaller than hesperornitheans and superficially resemble terns in size, proportions, and inferred habitats. Of the two, *Ichthyornis* is better known and shows a wider geographic distribution. Its fossils have been found from the Niobrara Chalk of Alberta, Alabama, Kansas, New Mexico, Saskatchewan, and Texas, in strata that were laid down in the Western Interior Seaway. Of several described species, only one, *Ichthyornis dispar*, is currently recognized (Clarke 2004). On the other hand, the holotype of *Apatornis celer*, known from an isolated synsacrum, has been transferred to anseriforms related to ducks and waterfowls (Hope 2002).

The skull of *Ichthyornis* was large and kinetic and the massive jaws, equipped with sharp, recurved teeth, were built for capturing and killing fish. The premaxilla and maxilla are virtually unknown in *Ichthyornis*, but the posterior part of the skull, quadrate, and tooth-bearing lower jaw are well represented. The skull is large relative to the rest of the skeleton (fig. 9.6B). It has a salt gland depression along the roof of the orbits, as seen in *Hesperornis*. The quadrate and temporal configurations are similar to those of modern birds, and the braincase is expanded. The jaws of *Ichthyornis* and *Hesperornis* show strong convergence because of a similar feeding adaptation. They probably relied heavily on fish. Both genera show similar tooth implantation. Teeth are set in a groove in young individuals but are fully socketed in adults. The teeth are present in the maxilla and dentary, where the crowns are compressed and recurved posteriorly, lacking serrations. There are about twenty-four teeth in each side of the jaw. The lower jaw has a well-developed intramandibular joint for lateral spreading of the rami. This mechanism allowed these birds to swallow a large amount of food. The two rami are separate and lack an ossified symphysis at the tip; however, the predentary bone is absent. The mandible has a coronoid bone but lacks a retroarticular process.

The cervical vertebrae of *Ichthyornis* have large pleurocoels and are weakly amphicoelous with prominent hypapophyses. They have moderately long, S-shaped necks and short trunks. The synsacrum contains ten vertebrae and there is a short and stubby pygostyle, which is plowshare-shaped possibly for attaching fan tail feathers. Most likely fan tail feathers provided extra lift and maneuver.

The morphology of the shoulder girdle and wing conforms to the pattern seen in modern flying birds. The scapula is narrow, and the coracoid is strut-like, with the development of a triosseal canal; distally, it is expanded to fit into a horizontal groove of the sternum. The sternum is strongly built, with a prominent keel cranially. The furcula is partly preserved and appears to be U-shaped. The short and stout trunk and large keeled sternum provided a rigid armature for attaching large flight muscles. The deep keel on the dorsolateral-facing glenoid, an acute angle between the articulation of the scapula to the coracoid, and a strong and strut-like coracoid with a large triosseal canal indicate that *Ichthyornis* was capable of powerful flapping flight. The large keel on the sternum suggests development of large flight muscles—the pectoralis and supracoracoideus—that provide the mechanical power for flapping flight.

The humerus is robust, with a prominent head and an enormous deltopectoral crest. Both dorsal and ventral tuberosities are well developed at the proximal end, with a distinct capital groove. Distally, the humeral condyles are modern looking, with a prominent brachial depression. The ulna has a trochlea at the distal end, and the carpometacarpus is totally fused. The interlocking carpal bones, the fused carpometacarpus, the reduction of digits and terminal claws, and a large extensor process in the innermost metacarpal clearly indicate the acquisition of powerful and complex flight strokes with deep wingbeats as in modern birds. The stubby thumb supports the alula; the second finger is by far the largest and robust on which are fastened the distal three or four primaries. The fused hand and finger bones provide strength and rigidity in the outer wing skeleton.

The pelvis and hindlimb of *Ichthyornis* are highly de-

rived, powerfully built, and modified to serve as landing gear. The pelvic girdle is greatly lengthened and welded to the synsacrum, and the ischium and ilium do not unite to form a symphysis but remain open to facilitate egg laying. The ilium has a long preacetabular process but a short postacetabular process. The ilium, ischium, and pubis are fused around a large, perforated acetabulum. The acetabulum contains a prominent antitrochanter. The ischium remains parallel to the ilium, without any contact such as that seen in ratites. The pubis is rod-like and reverted. Ventrally, the pubis and ischium remain separate, with a large pelvic outlet. Dorsally, the two ilia form a large pelvic shield.

The hindlimbs are strongly built for ground takeoff and landing. The femur is relatively short and cylindrical, with a prominent greater trochanter, fibular groove, and popliteal space. It is shorter than the stout tibiotarsus, and the metatarsus is completely fused. Like in modern birds, the femur was probably buried in the flesh; the tibiotarsus, tarsometatarsus, and three inner toes were the main weight-bearing bones, which were largely used for walking, leaping, ground takeoff, and landing. The hindlimb elements have a modern appearance, with a large degree of fusion at the joints to form the tibiotarsus and the tarsometatarsus. The tibiotarsus has developed both cnemial crests but lacks a supratendinal bridge at the distal end.

Among Mesozoic birds, *Ichthyornis* shows the most advanced flight structure comparable to that of modern birds and was capable of intricate maneuvering flight (see chapter 12). It was an acrobatic flier like modern terns with powerful wings, strong hands, a deeply keeled sternum, and a very short tail with a pygostyle. *Ichthyornis* was a tern-like shorebird about 24 centimeters long, was highly aerial and marine, and presumably caught fish on the wing in the Niobrara Sea by diving into water from the air. *Ichthyornis* developed large respiratory passages through the snout in front of the eyes that might have housed large scroll-like structures called turbinates for endothermy and improved physiology required for enduring flight. *Ichthyornis* flew over the large expanse of the Western Interior Seaway with its long and powerful wings. The bill is stout and heavy, slightly hooked, and equipped with numerous teeth in the maxilla and dentary, designed for capturing fish and crustaceans. In many respects, the flight apparatus of this 90 million-year-old bird resembles the basic structure of modern birds. It could glide and soar long distances, exploiting the wind shear of air currents above the waves in the oceans to provide lift. The wings are powerful, longer than they are wide, with the ulna longer than the humerus and the manus and bearing quill knobs for secondary feathers.

Although *Ichthyornis* shows a highly derived flight apparatus like that of modern birds, it shows several primitive features in the rest of the skeleton that suggests that this toothed bird was not immediately close to the ancestry of modern birds. These archaic features include toothed jaws; a maxilla larger than the premaxilla; an unfused jaw symphysis; amphicoelous cervicals; a bicondylar quadrate for the jaw joint; a primitive design of the synsacrum and pelvis lacking an ilioischiadic fenestra; and a less pneumatized skeleton.

Other Carinates

The fossil record of carinate birds from marine settings is much more widespread than that from terrestrial sediments. Recent discovery of fragmentary material of carinate birds from the Late Cretaceous of Patagonia and Belgium extends their range in continental environments. *Limenavis patagonica*, a Late Cretaceous carinate bird from the terrestrial sediments of Patagonia, is known from wing elements. *Limenavis* coexisted with several groups of dinosaurs and appears to be more derived than *Ichthyornis* on the basis of its wing structure. *Limenavis* is closer to the crown clade Aves than *Ichthyornis* and suggests that some carinates foraged in continental rivers and lakes. Similarly, tantalizing remains of another carinate bird, yet to be named, from the Late Cretaceous of Belgium may increase the geographic diversity of this group.

The Rise of Modern Birds

It is generally believed that Aves, or modern birds, had radiated entirely within the Cenozoic, following the extinction of dinosaurs, pterosaurs, and other archaic Cre-

taceous birds. Recent molecular and paleontological evidence suggests that they had a modest beginning in the Late Cretaceous time but diversified explosively in the Cenozoic soon after the KT extinction. Fragmentary fossils show that basal lineages of modern birds originated in the Late Cretaceous time and remained in low diversity before the KT extinction. Many of the Cretaceous avian taxa are represented by fragmentary or isolated elements, and their identities in specific groups remain uncertain. Among these Cretaceous assemblages, Hope (2002) and Dyke and Van Tuinen (2004) recognized valid specimens of several stem lineages of modern birds, including anseriforms (*Apatornis*, *Teviornis*, *Polarornis*); pelecaniforms (*Elopteryx*, *Trootix*); and doubtful remains of palaeognaths (lithornithid), galliforms (*Palintropus*, *Austinornis*), charadriiforms (*Cimolopteryx*, *Graculavus*, *Telmatornis*), procellariiforms (*Lonchodystes*), and psittaciforms. Not only is the majority of this material is incomplete, but in many cases age and provenance are dubious. Nevertheless, this scanty fossil record suggests the existence of a number of extant lineages of birds prior to the end of the Cretaceous. Although archaic birds (Enantiornithes and basal ornithuromorphs) dominated the Late Cretaceous ecology, the presence of several immediate avian outgroups (e.g., *Ichthyornis*, *Limenavis*, *Apatornis*) in the Late Cretaceous does imply that the lineage leading to extant birds must have differentiated prior to the end of the Cretaceous. From the limited fossil record, it appears that some basal lineages of modern birds such as galliforms, anseriforms, loons, and cormorants were present from the Late Cretaceous time on and survived into the Tertiary little changed. Most of the stem lineages of modern birds originated in aquatic habitats of the Cretaceous, but some gamebirds probably ventured onto land. The presence of anseriforms in the Late Cretaceous implies the presence of their sister-group galliforms at the time because these two lineages originated from a common ancestor of all Galloanserae (see chapter 11).

Polaronis from Antarctica

One of the most contentious issues in avian paleontology is when and where the Aves, or modern birds, arose. Gondwana has been recognized as a major center of origin of modern birds prior to the KT extinction on the basis of molecular phylogeny, anatomical evidence, and paleobiogeography. Recent discovery of loons, or anseriforms, and charadriiforms in the Late Cretaceous deposits of Antarctica supports the origin of the modern waterbird assemblages in the southern polar region. Among these finds, the most complete Cretaceous Aves is *Polarornis gregorii* from the Late Cretaceous Lopez de Bertodano Formation of Seymour Island of Antarctica (Chatterjee 2002). *Polarornis* represents the first skeleton complete enough to be placed unambiguously within a modern clade of Aves.

Polarornis shows several hallmarks of Aves, including fused cranial bones, edentulous jaws, and the presence of three articular facets on the ventral end of the quadrate. The skeleton of *Polarornis* was found in sandstone deposits along with plesiosaurs, mosasaurs, and ammonites, indicating shallow marine environments. The holotype specimen is known from an associated partial skeleton including a skull, four articulated cervical vertebrae, a sternal fragment, a complete left femur and a partial right femur, and half of the left tibiotarsus. Initially, *Polarornis* was identified as the oldest loon. In size, proportion, and morphology, *Polarornis* resembles the common loon *Gavia immer*. Subsequent discoveries of additional postcranial material from the Antarctic Peninsula, as discussed later, questions the affinity of *Polarornis* as a basal member of Gaviidae (loons), and may shift it to diving members of anseriforms (ducks) among modern birds.

The skull of *Polarornis* is fairly intact, beautifully preserved, and entirely edentulous, but the tip of the beak, the dorsal part of the braincase, and the lower jaw are missing. It has a long and tapering snout and intimately fused dermal bones. The external naris is elliptical and holorhinal and has been shifted considerably backward with the development of a typical beak (fig. 9.7A). The frontal process of the premaxilla is elongate and extends considerably backward to contact the frontal, thus displacing the nasal laterally, where it overlaps the rostral end of the mesethmoid. The nasal is a small peripheral bone forming a slanting bar between the external naris

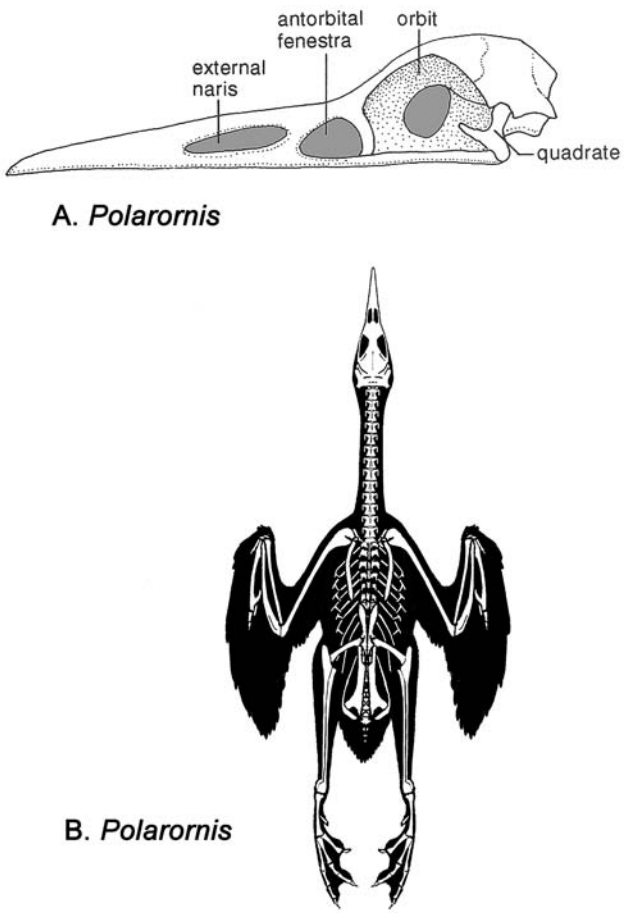


Figure 9.7. The modern bird *Polarornis* from the latest Cretaceous of Antarctica, which probably belonged to a stem group of foot-propelled anseriforms. A, skull in lateral view; B, reconstructed skeleton in dorsal view, estimated length 60 centimeters (after Chatterjee 2002).

and the antorbital fenestra. The frontonasal hinge area is very similar to that of modern prokinetic birds. The antorbital fenestra is triangular, bounded posteriorly by the sloping lacrimal, which fails to reach the narrow jugal bar. The orbit is very large, circular, and forwardly placed. Along the roofs of the orbit are well-marked depressions for the salt glands. The orbital septum is fully ossified. The squamosal is reduced and forms an overhanging roof over the quadrate. Ventrally it has a cotyle for the lateral head of the quadrate. The palate is of the neognathous type, with the development of palatine-pterygoid mobility. This is the earliest documentation of a neognathous bird (similar to modern flying birds) in the fossil record. The quadrate shows all the attributes of streptostyly with a large orbital process, and its articular end shows two distinct heads for the squamosal and the prootic, respectively. Laterally, the quadrate has a deep socket for the reception of the quadratojugal. The otic capsule of the braincase is very similar to that of a modern loon with the development of anterior, posterior, and dorsal tympanic recesses. Like modern birds, the skull of *Polarornis* shows all the morphological correlates of prokinesis. A CT scan of the cross section of the narial region in front of the eyes of *Polarornis* shows the voluminous space for respiratory turbinates, which are scrolled bones or cartilages correlated with endothermy. Living birds have all respiratory turbinates.

Four articulated cervical vertebrae of *Polarornis* are preserved in the collection. They are elongated and heterocoelous, with ribs fused to them. A strong hypapophysis on the centrum terminates cranially against a ventral depression. The wings and girdles are missing in the specimen. The femur is twice the size of that in the modern loon. The head is spherical, directed medially with a long constricted neck, and contains a circular pit for the insertion of the capital ligament. The tibiotarsus is long and its cnemial crest is strongly developed, indicating that *Polarornis* had already acquired the foot-propelled diving adaptation.

The anatomical information on *Polarornis* has been supplemented recently by the discovery of another exquisitely preserved three-dimensional skeleton from the Late Cretaceous strata of the nearby Vega Island of the Antarctic Peninsula (fig. 9.7B). Currently, I am collaborating with Julia Clarke and Fernando Novas to study this new specimen of *Polarornis* and assess its phylogenetic position in the tree of modern birds. The new specimen is about the size of a red-throated loon, represented largely by an articulated postcranial skeleton. It is considerably smaller, more gracile, and more slender than its sympatric species *Polarornis gregorii*. Among the cranial material, a left pterygoid and a caudal portion of the right mandible are preserved. The pterygoid is relatively short, complete with expanded ends, showing flexible joint surfaces for the palatine and quadrate. The manidibular cotylar fossae

are complex as in modern birds for articulation with the three articular facets of the quadrate. Five associated anterior cervicals, seven associated thoracic segments, and three free caudals are preserved. The presacral centrum is heterocoelous and bears a large ventral hypapophysis, and the neural spine is proportionately large. The first thoracic has a short neural spine, but the last thoracic vertebrae show some degree of consolidation.

The intact wing and shoulder girdle of the gracile specimen suggests that *Polarornis* had also developed sophisticated powered flight. The scapular blade is narrow, but thickens anteriorly where it articulates with the coracoid by a ball-and-socket joint and forms a triosseal canal. The coracoid is short, robust, and strut-like with the development of both procoracoid and acrocoracoid processes. The humerus is a long and slender bone with a highly expanded proximal end with a prominent convex head with a deep bicipital furrow below it. The bicipital surface is a convex swelling; in the posterior aspect is a large pneumatic fossa. The conjoined radius-ulna is represented by natural molds; they are smaller than the humerus. The two carpal bones, the radial and ulnar, are complex bones resembling those of extant birds and performed similar crucial functions during flight. The carpometacarpus is completely fused; the phalangeal formula is 1-2-1. The femur is relatively long and slender. The tibiotarsus shows a long cnemial crest as in diving birds. A separate patella has been found in this specimen that would increase the length of the cnemial crest but makes the affinity of *Polarornis* with loons questionable because loons lack a patella. A metatarsus is almost concealed in the matrix except for the distal extremities of the third and fourth trochlear pulleys, which are highly compressed sideways for foot-propelled swimming.

The wings and hindlimbs show two distinct locomotor modules in *Polarornis*: aerial locomotion by the wings and aquatic locomotion by the hindlimbs. Like modern grebes, loons, and diving ducks, *Polarornis* could move in both air and water. The proportions of wing elements are primitive, with the humerus longer than the ulna and the ulna longer than the manus. Because of diving adaptations, the bones became nonpneumatic and dense to increase the bird's weight for submergence. As a result, *Polarornis* had small wings with high wing loading and had to fly faster with rapid wingbeats to remain airborne. I have calculated the flight performance of the gracile *Polarornis* through a computer simulation model. The performance analysis suggests that it was capable of continuous flapping flight with a cruising speed of 50 kilometers per hour. The flying performance of *Polarornis* is not impressive because of high wing loading. There was a tradeoff between decreased powered flight and increased diving ability.

The hindlimb elements of *Polarornis* exhibit specializations for aquatic locomotion that are characteristics of foot-propelled diving birds: dense, heavy, nonpneumatic bones; a streamlined body; a short femur with a double hinge-like articulation at and above the acetabulum; a long tibiotarsus with a pronounced cnemial crest; and a laterally compressed tarsometatarsus. The femur was held horizontally at the hip joint, while the tibiotarsus was directed backward parallel to the body axis and was fixed at the knee joint by bony articulations and powerful muscles. In foot-propelled birds, the relative lengths of the leg bones should reflect the degree of specialization for swimming and diving. *Polarornis* has a relatively long femur and a correspondingly short tibiotarsus with a reduced cnemial crest compared to those of living loons. The femur of *Polarornis* is about 46% of the length of the tibiotarsus, whereas in living loons, this ratio is about 25%. Since the femur is sticking transversely sidewise, the relatively long femur in *Polarornis* would make the body much wider, like that of ducks, increasing the surface area, whereas in living loons, the body is extremely narrow, streamlined, and spindle shaped for diving, as the femurs are considerably reduced to bring the feet closer to the body. Like in modern foot-propelled birds, the femur and tibiotarsus were probably enclosed by muscle and skin and were held largely immobile (fig. 9.7B). The functional joint during swimming and diving was at the ankle. The long cnemial crest on the tibiotarsus was primarily used for the attachment of the gastrocnemius muscles, the major extensor of the foot. The extensor muscles are united just above the heel, to the strong

tendon, and inserted at the back of the proximal part of the tarsometatarsus. With these muscles, *Polarornis* would be capable of moving its feet backward with great force when bending at the heels. During the recovery stroke, as the foot would move forward with toes flexed and abducted to reduce drag, the greatly compressed tarsometatarsus would glide through the water like a knife to minimize water resistance. Foot-propelled birds have large feet with three front toes fully webbed like a large blade of an oar; the tarsus is flattened to form its central part so that it moves easily through the water. They use their feet alternately while surface swimming and simultaneously while diving underwater. Perhaps *Polarornis* used a similar strategy during aquatic locomotion. The hindlimbs of *Polarornis* were less specialized for diving than those of living foot-propelled birds, as indicated by its relatively long and slender femur and short cnemial crest. *Polarornis* appears to have been a surface swimmer but less specialized for underwater diving.

Clarke et al. (2005) described *Vegavis iaai* from the Late Cretaceous Vega Island, where the gracile form of *Polarornis* was found. *Vegavis* is known from disarticulated elements of the postcranial skeleton including isolated vertebrae, a scapula, a humerus, an ulna, pelvic bones, a fibula, and a tarsometatarsus and was classified as an anseriform, more specifically, a duck. Comparison of *Vegavis* with the gracile *Polarornis* indicates they are identical; *Vegavis* is a junior synonym of *Polarornis*. With additional information from *Vegavis* and the identification of a patella in the gracile skeleton, the taxonomic placement of *Polarornis* within Gaviidae is problematic. *Polarornis* could represent a diving duck, or even the flying ancestor of a primitive penguin lineage. Our ongoing work may clarify the systematic position of *Polarornis*.

Another duck-like bird from the Late Cretaceous Gobi Desert of Mongolia is *Teviornis gobiensis*, represented by partial wings. Unlike *Polarornis*, *Teviornis* lived in lakes and rivers of the Gobi in semiarid environments. It thus appears from paleontological evidence that modern birds originated in the Late Cretaceous and rebounded and explosively radiated in the Early Tertiary after the extinction of the pterosaurs.

10 The End-Cretaceous Mass Extinction

Thou wast not born for death, immortal Bird!
No hungry generations tread thee down;
The voice I hear this passing night was heard
In ancient days by emperor and clown.

John Keats, *Ode to a Nightingale*, 1819

Extinction and Renewal of Life

Extinction is forever. It is a process that has occurred since life appeared on Earth. It is estimated that 99% of the plant and animal species that have ever lived on Earth are now extinct. Mass extinctions have, at times, globally exterminated more than half of living organisms in a geological blink of an eye. Five major episodes of mass extinction have occurred during the past 500 million years: Late Ordovician (440 million years ago), Late Devonian (305 million years ago), Late Permian (245 million years ago), Late Triassic (210 million years ago), and Late Cretaceous (65 million years ago). Mass extinctions are the benchmarks of the geological time scale because they create great shifts in biotic composition that are conspicuously recorded in the stratigraphic record. These great breaks in the continuity of fossil record manifest evidence that millions of species were extirpated within brief mass extinction time frames. Hotly debated, these extinctions are attributed to a host of causative agents: pollution from massive volcanism, plate tectonics, comet and asteroid impacts, rapid climatic or environmental changes, and numerous other alternatives.

Mass extinctions may be the primary force for major shifts in life's history. When a mass extinction strikes, it is not necessarily the most fit that survive, but merely the most fortunate. Mass extinction is an accelerated version of natural selection at such a fast pace that organisms have little time to adapt amid environmental catastrophe. After each mass extinction, life rebounds, is revamped, and diversifies. Many dominant groups in the pre-extinction period are eliminated to provide opportunities for surviving lineages to proliferate. Out of such biotic crises a new world order is born. Mass extinctions change the rules of evolution by removing successful incumbents and encouraging the meek to proliferate.

Of these five mass extinctions, the KT (Cretaceous-Tertiary) boundary extinction, when a global catastrophe killed off dinosaurs and more than half of life on Earth in a geological instant 65 million years ago, is the most recent and has yielded much more infor-

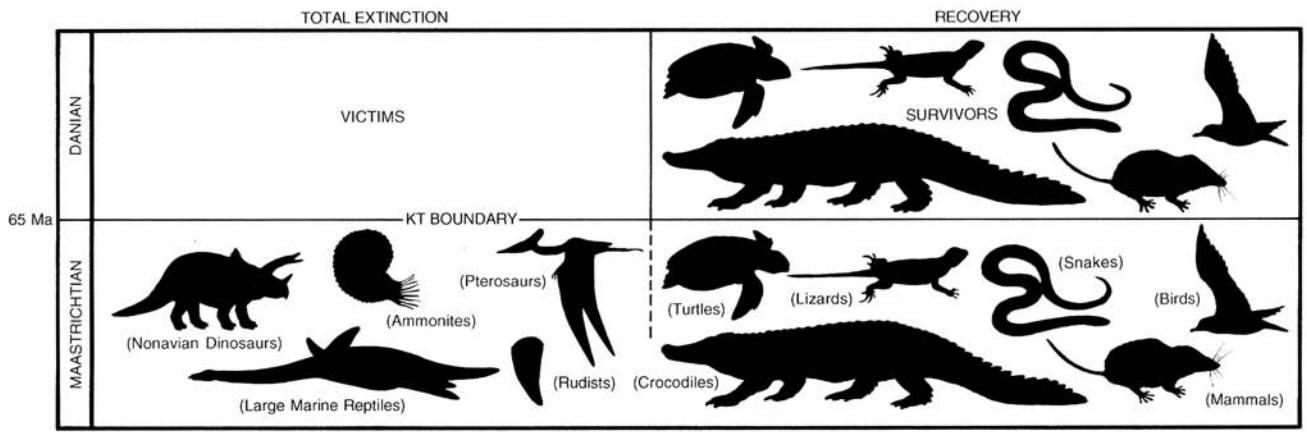


Figure 10.1. Victims and survivors after the KT extinction. The primary victims were nonavian dinosaurs; pterosaurs; large marine reptiles, such as plesiosaurs and mosaaurs; and various invertebrates, such as ammonites and rudists. Lizards, snakes, turtles, crocodiles, birds, and mammals endured this catastrophe and radiated. After this crisis both birds and mammals underwent explosive evolution in the Tertiary.

mation than any of the others. It is also the most famous. On land, magnificent dinosaurs, soaring pterosaurs, flying enantiornithine and ornithurine birds, and many species of plants vanished forever. In the oceans, there were severe extinctions of planktonic foraminifera (microscopic abundant shelly plankton), major reef-building bivalves called rudists, spiral-shaped ammonites, and their close relatives belemnites; many species of brachiopods, echinoids, and fish as well as two-thirds of all marine species were also extinguished.

The sudden extinction of nonavian dinosaurs at the end of the Cretaceous period has puzzled both scientists and the public for more than a century. Having survived for 160 million years, dinosaurs seemed indestructible. During that relatively brief period, all land animals weighing more than 25 kilograms disappeared from the planet. All pterosaurs, plesiosaurs, and mosasaurs, as well as several families of birds and marsupial mammals and hundreds of plants, were also suddenly wiped out. The Earth was devastated. Life was ravaged by one of the worst catastrophes imaginable.

There were survivors, of course. Modern birds, placental mammals, crocodiles, turtles, lizards, and snakes all survived as groups—despite the extinction of some species (fig. 10.1). The selectivity of extinction is not fully understood. Small body size, a large number of individuals, fossorial habits (living in burrows like bunkers), or freshwater adaptations might have played a selective role in survival of species across the KT boundary. All mass extinctions, however, have been followed by regenerative intervals of recovery with the novel life forms to open new ages in which the numbers of species on Earth burgeon once again (Stanley 1987). The KT extinction opened ecological opportunities for the radiation of two important vertebrate clades we see around—placental mammals and modern birds—which occupied the vacant niches left by dinosaurs on land and pterosaurs in air, respectively. Whatever the cause of the KT extinction, the aftermath was clear: the modern birds emerged as the dominant aerial vertebrates at the end of the Cretaceous period as the sole surviving lineage of dinosaurs. So do the placental mammals that reclaimed the terrestrial niches of dinosaurs.

What catastrophe led to such an unprecedented ecological crisis? Currently, two competing models have emerged to explain this apocalyptic disaster at the KT boundary: the meteorite impact hypothesis and the volcanic hypothesis. The impact theory postulates that twin asteroids hit the Earth—one in Mexico, the other in India—at the end of the Cretaceous that led to the final demise of dinosaurs and other species on land and sea. The volcanic theory argues that pollution in the atmosphere and

oceans due to the massive outpourings of Deccan flood basalt in India had a devastating effect on global ecology and the environment.

Impact Model

A key breakthrough in the KT mass extinction debate occurred in 1980, when the physics Nobelist Luis W. Alvarez and his geologist son, Walter Alvarez, both of the University of California at Berkeley, with their nuclear chemist colleagues Frank Asaro and Helen V. Michel discovered unusually high concentrations of the rare metal iridium—50 to 100 times the normal levels—from a 2.5-centimeter-thick clay layer at the KT boundary marine section lying between limestone beds hundreds of meters thick in a gorge outside the medieval city of Gubbio, Italy. The thin, pinkish clay bed was formed at the time of the extinction of dinosaurs, about 65 million years ago, and can easily be demarcated in the section with the naked eye: the large Cretaceous planktonic foraminifera *Scaglia* that characterizes the Upper Cretaceous beds suddenly disappears above the iridium-rich clay layer. The sudden foraminiferal extinction in the essentially complete KT boundary section in Gubbio led the Alvarez group to believe that the KT mass extinction was a catastrophic event. But what was the cause of the catastrophe? Such a large amount of iridium in KT boundary clay is puzzling. Iridium is rare in the Earth's crust but is relatively abundant in some asteroids, particularly in primitive stony meteorites known as carbonaceous chondrites. The Alvarez team also detected the iridium anomaly at the KT boundary section of Stevens Klint, south of Copenhagen in Denmark, and argued convincingly that the source of the iridium spike in these KT marine sections must be extraterrestrial and derived from the vaporization of an impacting meteorite, which dispersed an unearthly concentration of cosmic iridium around the globe that settled out of a global dust cloud kicked up by the impact. They concluded that a giant asteroid, about 10 kilometers in diameter, hit the Earth and produced a circummundane dust cloud that blocked the Sun, chilled the planet, and killed the dinosaurs and other organisms. They speculated that the collision would have left a crater about 200 kilometers in diameter and argued that there should be similar concentrations of iridium at different KT boundary sites in both continental and marine sections. Other researchers confirmed the iridium anomaly as a worldwide feature and began to find other evidence for a KT impact. Within a decade, more than one hundred such iridium anomalies were discovered at KT boundary sections all over the globe.

The impact theory was strengthened by three additional independent forms of evidence in the KT boundary sediments in different parts of the world: (1) quartz grains with deformation produced by shock during impact (Bohor et al. 1987); (2) spherules representing droplets of impact melts (Smit 1999); and (3) carbon soot particles resulting from global fires (Wolbach et al. 1988). Shocked quartz is a distinctive signature of an impact event, as it can form only at a force of more than 10 gigapascals that travels through quartz-bearing grains of the target rock to produce microscopic shock lamellae. Spherules have also been detected at this boundary. They represent droplets of molten rocks thrown into the atmosphere during the impact event. Sediments at the KT boundary often include a layer of soot particles, which may be the residue of vegetation burned during widespread wildfire caused by the impact. The wildfire would have consumed oxygen and poisoned the atmosphere with carbon monoxide. Along with ejecta components, a fern spike in many terrestrial KT boundary sections indicates an abrupt shift in pollen ratios from an angiosperm-dominated to a fern-dominated ecosystem after major forest fires.

The Chicxulub Crater

When the Alvarez group presented their iridium spike in 1980 as the cardinal evidence for an impact event at the KT boundary, reinforced by additional mineralogical analysis of ejecta deposits such as shocked quartz, spherules, and carbon soot, a widespread search for the proposed impact crater took place over the following decade. The absence of a crater of suitable size and right age was a problem for the Alvarez group. In the mid-1980s, more than 120 terrestrial impact craters had been discovered on Earth, and several new craters were being

identified each year, but most were too small; only two known craters approached the size predicted by the Alvarez group: Sudbury in Canada (~ 200 kilometers) and Vredefort in South Africa (~ 140 kilometers). Both were more than 1.8 billion years old, much older than the age of the KT boundary, and were irrelevant to the debate.

Eventually, the KT impact ejecta led to the crime scene. It was a remarkable detective story with contributions from hundreds of geologists all over the world. It was soon realized that the size and abundance of the ejecta such as shocked quartz grains and the spherule layer in North America, especially around the Gulf of Mexico, as well as impact-generated tsunami deposits reported from the KT boundary sections of the Brazos River of Texas and Braggs of Alabama might give some clue to the location of the crater within the North American continent, particularly around the Gulf of Mexico–Caribbean region (Bourgeois et al. 1988). This prediction was reinforced by the discovery of the 180-kilometer-diameter Chicxulub crater structure on the northern margin of the Yucatán Peninsula, Mexico, which was buried under 1,100 meters of carbonate strata—half on land and half on the sea floor. The circular feature in the Yucatán had been known for years in the oil industry. The Chicxulub crater, the result of a truly catastrophic geological event, is a ring-like structure, about 180 kilometers in diameter, first reported by Glen Penfield and Antonio Camargo of Pemex, the Mexican national petroleum company, and later geophysically confirmed by Alan Hildebrand and his mentor William Boynton of the Canadian Geological Survey (Penfield and Camagro 1982; Hildebrand et al. 1991). They showed that the Chicxulub crater has a typical morphology of a complex crater with a central peak, surrounded by an annular basin and a faulted outer rim. Hildebrand, Boynton, and others later reported shocked quartz drill core samples from Chicxulub that helped verify its impact origin. They further documented chemical and isotopic similarities between impact melts of target rocks (andesites) and proximal ejecta from the KT boundary sections of Haiti and Mexico (Hildebrand et al. 1995). Finally, Buck Sharpton of the Lunar and Planetary Institute in Houston and his colleagues reported argon-argon radiometric ages for the andesites from the drill core samples that showed that the Chicxulub crater was formed right at the KT boundary, 65 million years ago (Sharpton et al. 1992). The presence of shocked quartz, impact melt, brecciation, the KT boundary age of the basin, a gravity anomaly, and iridium enrichment within the crater itself is compatible with an impact origin for the Chicxulub structure (Hildebrand et al. 1991). If Chicxulub is indeed a very large KT impact scar, extensive deposits of impact ejecta and tsunami deposits should surround it. This is indeed the case (Bourgeois et al. 1988). The distribution of proximal ejecta components and tsunami deposits at the KT sections in Haiti, Mexico, Texas, Alabama, the Caribbean, and adjacent areas strengthens the argument for a point of collision at Chicxulub (fig. 10.2).

The Shiva Crater

A second ominous crater, the Shiva crater, about 500 kilometers in diameter, has been identified in the Mumbai Offshore Basin on the western continental shelf of India. The Mumbai Offshore Basin, a giant petroleum entrapment, is an enigmatic, Atlantic-type passive margin, and should be tectonically stable and aseismic like any other passive rift margin. In reality, the Mumbai Offshore Basin is highly seismic, chaotic, and geodynamically anomalous with a highly deformed and sheared lithosphere, which are testaments of a traumatic history of tortured landscape. Om Prakash Pandey and Pradeep Agarwal of the National Geophysical Research Institute (NGRI) of Hyderabad have linked the geophysical anomaly of the western shelf to a major impact event at the KT boundary (Pandey and Agarwal 2001). They observed near Mumbai that the lithospheric mantle has been considerably sheared and deformed; the crust-mantle boundary has been uplifted more than 50 kilometers and shows unusually high heat flow. These authors have attributed this unusual rise of the Moho boundary and the geothermal anomaly (heat flow greater than 80 m watt/m^2) on the western shelf to an impact event (fig. 10.3). Like Pandey and Agarwal, Chris Hartnady of the University of Cape Town, South Africa, argued that the enormous force of a large impact on the western coast of India shattered the

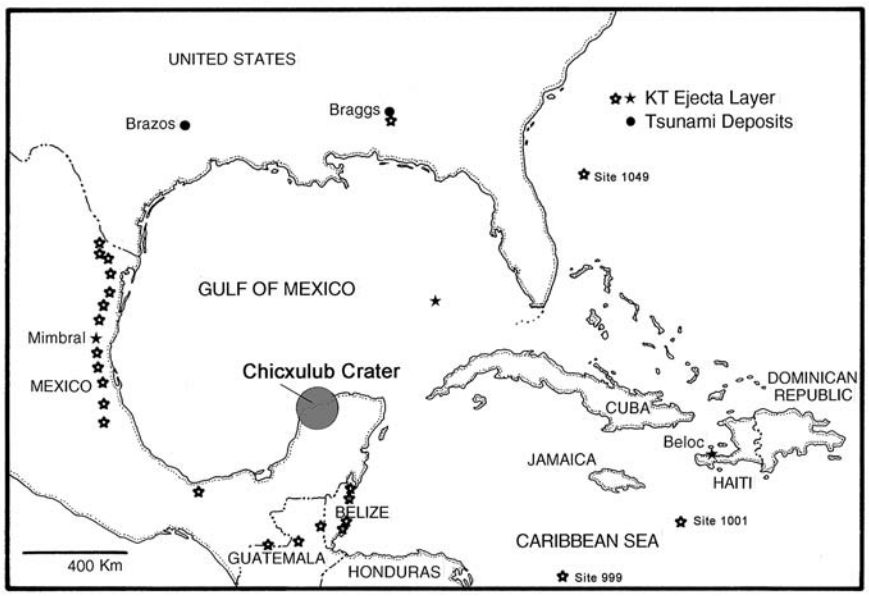


Figure 10.2. Location of the Chicxulub crater on the northern edge of the Yucatán Peninsula, Mexico, showing the distribution of the KT boundary sequences of proximal ejecta and tsunami deposits around the Gulf of Mexico, the Caribbean Sea, and the Atlantic Ocean.

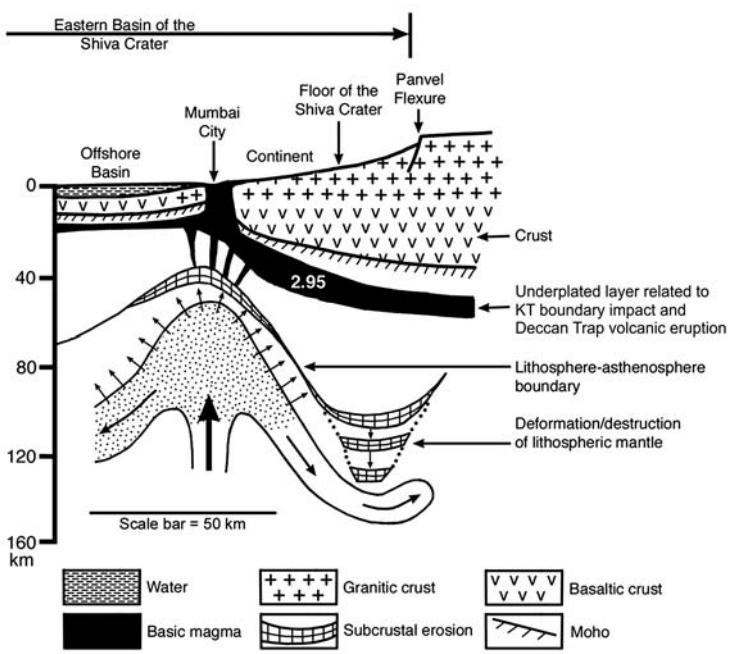


Figure 10.3. Schematic diagram of the eastern part of the Shiva crater near the Mumbai coast showing the upwarping of the mantle more than 50 kilometers and the possible deformation and destruction of the lithosphere because of the Shiva impact; on the right side of the drawing, east of Mumbai City, the thick Deccan Trap has been removed to show the floor of the Shiva crater (modified from Pandey and Agarwal 2000; Chatterjee et al. 2006).

lithosphere, rifted the Seychelles block from the Indian plate at KT boundary time, and triggered a large-scale reorganization of plate boundaries in the Indian Ocean (Hartnady 1986). Dave Alt and his associates from the University of Montana speculated that a major impact on the west coast of India might have created not only an enormous crater of about 600 kilometers in diameter, but also induced pressure-release melting in the asthenosphere to trigger the great Deccan volcanism. Basalt then filled the crater basin to form an immense lava lake, the terrestrial equivalent of lunar mare (Alt et al. 1988). Janardan Negi and his colleagues of the NGRI of Hyderabad suggested that the Deccan Traps are the result of a major impact in the vicinity of Mumbai (Negi et al. 1993). Walter Alvarez and Frank Asaro are among those who have speculated on a KT impact site beneath the Deccan Traps (Alvarez and Asaro 1990). All these workers, however, did not specify the exact location of the impact site on the Indian west coast, but they did allude to a possible impact event before I discovered and named the Shiva crater around Bombay High in 1992 (Chatterjee 1992b).

The crater is largely submerged and buried by a 2- to 7-kilometer-thick strata of postimpact Tertiary sediments on the western shelf of India, but the eastern part of the crater rim, the Panvel Flexure, comes onshore along the Mumbai coast and is tectonically seismic and active, punctuated by hundreds of hot springs (fig. 10.4). The central region of the crater lies in the Arabian Sea around Bombay High, which is an enigmatic submarine mountain 4 kilometers high. The Bombay High Basin is the largest hydrocarbon field in India. The Oil and Natural Gas Corporation (ONGC) discovered and studied the basin in detail using geophysical and deep drill core data, which are described in several scientific publications and internal reports (Rao and Talukdar 1980; Basu et al. 1982; Bhandari and Jain 1984; Mathur and Nair 1993; Zutshi et al. 1993). However, the geologists of the ONGC did not realize that they were mining oil and gas from the largest crater on Earth.

The Shiva structure is a complex multiring basin with a peak ring of subsurface mountains, including Bombay High, Mukta High, Panna-Bassein High, Heera High, and several other unnamed peaks, which stand several kilometers above the Precambrian basement rock (fig. 10.4). The peak rings consist of Deccan Traps and Neoproterozoic granite cores, which were rebounded by the bolide impact. The peak ring is about 250 kilometers in diameter, and is surrounded by an annular trough containing 2- to 7-kilometer-thick postimpact sediments ranging in age from Paleocene to Pliocene. Finally, the annular basin is bordered outside by an elevated and faulted crater rim. The architecture of the Shiva basin bears all the hallmarks of a large, complex, multiring crater. A superpowerful pressure wave created by the Shiva impact shattered the crust of western India, created radial rift basins and earthquake epicenters, and rifted and separated Seychelles Island from India. The impact could have rattled the magma chamber in the interior of the Earth and enhanced Deccan volcanic activity.

Geophysical evidence and drill core samples suggest that the Shiva crater formed around 65 million years ago. Indirect evidence of an impact, such as the iridium anomaly, shocked quartz, and spherules have been reported from different KT boundary sections around the Shiva crater. Gravity data of the Shiva crater show a major gravity low anomaly over the central peaks of the Bombay High region similar to the pattern of the Chicxulub crater. The peak ring has a clear gravitational signal of an impact crater. Using several cross sections of the Bombay High oilfield, I have reconstructed the three-dimensional morphology of the Shiva crater. However, critical borehole data are essential to confirm the impact origin of the Shiva structure. The ongoing Deep Scientific Koyna Drilling Project near the eastern rim of the Shiva crater may provide valuable insights about the genesis of the structure.

Using the scaling equation (Melosh 1989), the 500-kilometer-diameter Shiva crater suggests an impact projectile of 40 kilometers in diameter, about the size of the Near Earth Asteroid (NEA) Ganymed. The target rocks of the Shiva impact consist of bilayered, rheologically variable Proterozoic granite and Deccan basalt, which were shattered, melted, and rebounded. As a result, the fluid ejecta from melt rocks were emplaced ballistically

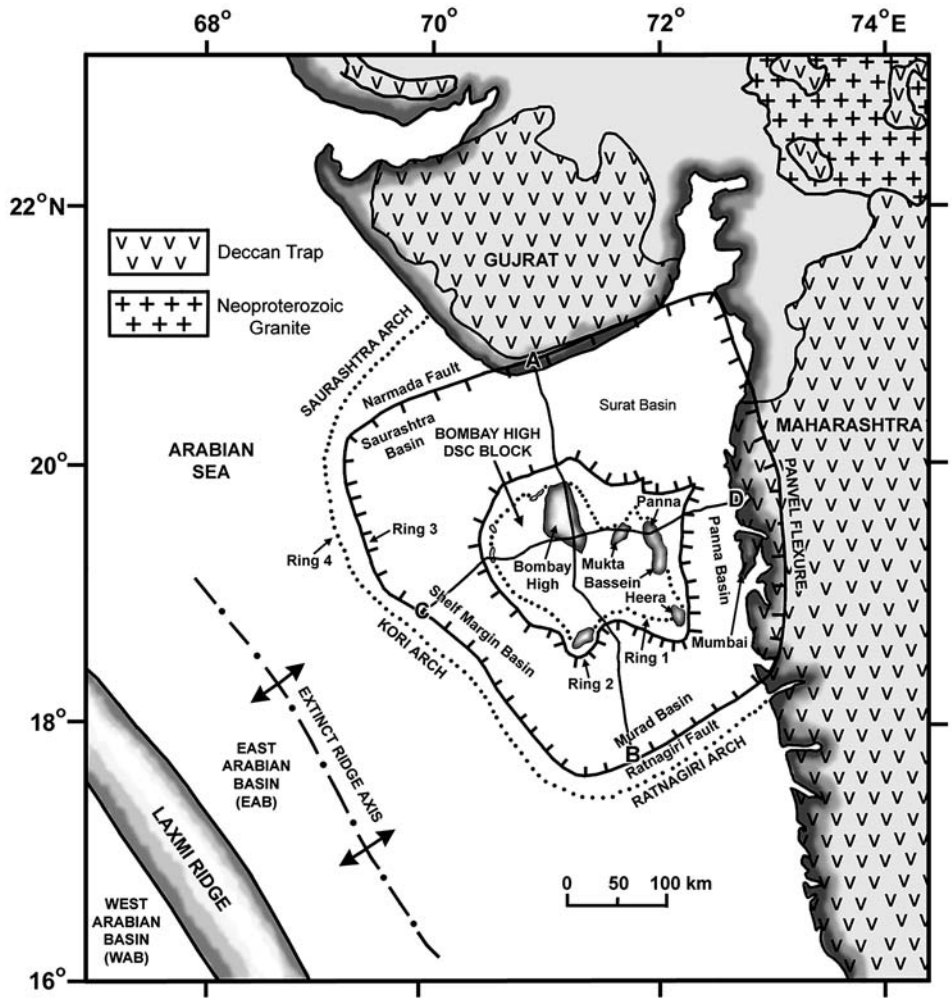


Figure 10.4. Present-day location of the Shiva crater at the Mumbai Offshore Basin, western shelf of India. The Shiva structure is a complex peak ring crate and a multiring basin, about 500 kilometers across, which is buried by 2- to 7-kilometer-thick, postimpact Cenozoic sediments. The crater ring is defined by a peak ring, an annular trough, and the faulted outer rim. A small segment of the eastern part of the crater lies near the Mumbai coast, which is bordered by the highly seismic Panvel flexure; here the crater floor is overlain by 2-kilometer-thick Deccan Traps. The peak ring is about 250 kilometers in diameter and consists of several central uplifts, including Bombay High, Mukta High, Panna-Bassein High, Heera High, and several unnamed peaks, caused by the rebound of crustal basement following impact (after Chatterjee et al. 2006).

along the northeast downrange direction. Subsurface stratigraphy of the Shiva crater is known primarily from petroleum exploration drill holes and seismic stratigraphy. The postimpact strata are horizontal Paleocene to Pliocene beds overlying a thick brecciated layer formed by the impacting process. The brecciated horizon is sandwiched between the Deccan Traps below and the Early Paleocene Panna Formation above and contains fragments of bilayered target rocks, namely, Proterozoic granite and Deccan Traps. The Deccan Traps and Panna Formation bracket the age of the crater basin right at the KT boundary, around 65 million years ago (fig. 10.5).

Although hypervelocity impacts normally create circular craters, such impacts at a low angle (~15° from the horizontal) often generate elongate craters such as the Messier and Schiller craters on the Moon and two unnamed twin craters on Mars with teardrop shapes at the downrange (fig. 10.6). The azimuth of the tip of the teardrop of the

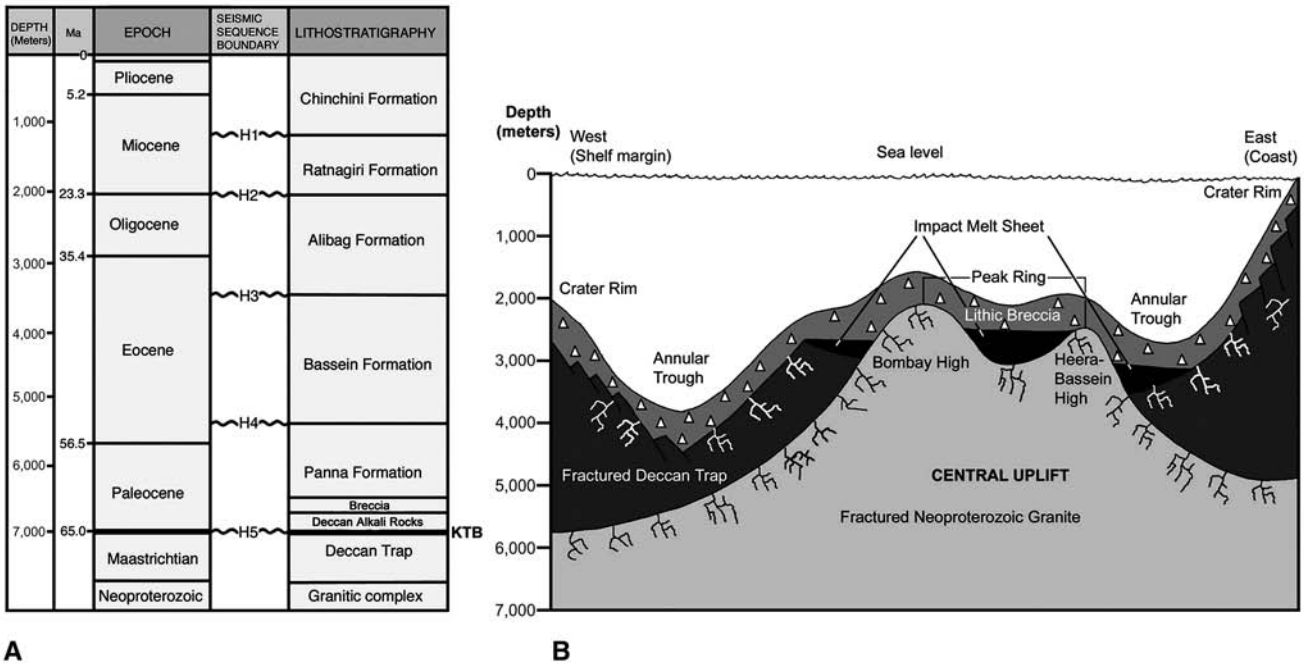


Figure 10.5. A, generalized stratigraphy of the Shiva crater. The target rock was bilayered Proterozoic granite and Maastrichtian Deccan Trap. The oldest postimpact sedimentary units in the crater basin include the impact breccia followed by the Early Paleocene Panna Formation. The Panna Formation and Deccan alkali rocks bracket the age of the crater around KT boundary time. B, schematic stratigraphic section of the Shiva crater along the west-east dimension from drill core data to show the relief of the crater basin; the overlying postimpact Cenozoic sediments were removed (after Chatterjee et al 2006).

Shiva crater indicates that the downrange direction of the Shiva bolide was northeast. The Shiva bolide flew obliquely from the southwest, over South Africa, the Arabian Sea, and Seychelles Island, before hitting the western shelf of India at roughly a 15° angle.

If Shiva is indeed a very large impact crater, one should expect extensive deposits of ejecta emplaced ballistically at the KT boundary layer proximate to the crater. However, during the KT boundary impact event, extensive Deccan lava was also erupting in adjacent areas that covered 800,000 square kilometers in west-central India and must have engulfed and obliterated thick deposits of proximate ejecta components. Only rarely would ejecta layers be preserved outside the Deccan volcanic province several hundred kilometers distant from the crater.

There are several KT boundary sections in India, particularly around the perimeter of the Deccan volcanic province, which have yielded several ejecta components in a northeast trajectory attributed to the Shiva impact (fig. 10.7). The proximal fluid ejecta within the Deccan province are preserved in the form of large mountain-like spires of alkali igneous rocks. The distal ejecta include shocked quartz, iridium anomalies, highly magnetic nanoparticles, fullerenes, magnetic spherules, nickel-rich spinels, and Deccan basalt spherules.

The Shiva impact might have triggered the widespread distribution of the Deccan alkali volcanism as fluid ejecta that occurred during the late phase of Deccan volcanism. Deccan alkali rocks have been reported both from inside and outside the crater. These impact melt rocks are rich in iridium because of contamination from impacting meteorites (Shukla et al. 2001) and were formed precisely 65 million years ago (Basu et al. 1993). In contrast, the Deccan basalt is poor in iridium content and has a prolonged volcanic history that occurred during an interval spanning about 3 million years across the KT boundary (Keller 2012). Outside the Shiva crater, the colossal volcanic plugs of melt rocks are arranged radially at Anjar, Kadi,

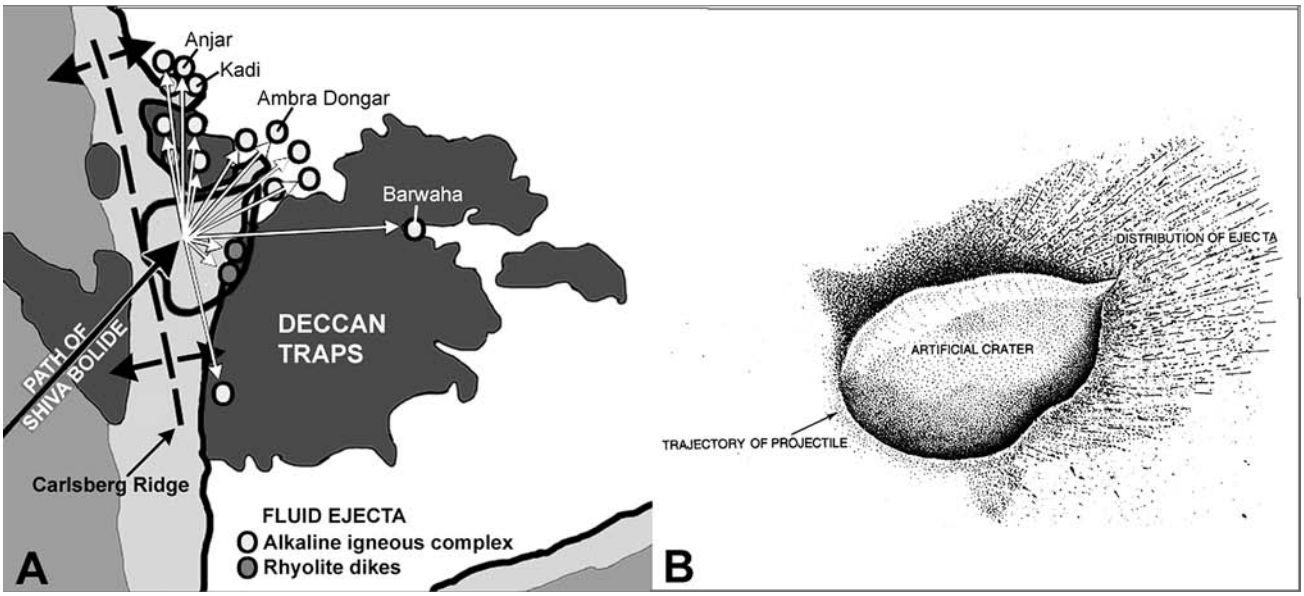


Figure 10.6. A, radial, asymmetric distribution of fluid ejecta (Deccan alkali rocks) downrange of the Shiva crater; the morphology of the crater with a teardrop shape and the asymmetric distribution of melt rocks are consistent with a low-angle oblique impact model along the northeast downrange direction. B, artificial crater produced by low-angle (~ 15°) oblique impact in the laboratory, which mimics the shape and fluid ejecta distribution of the Shiva crater (modified from Schultz and Gault 1990; Chatterjee et al. 2006).

Jawahar, Phenai Mata, Amba Dongar, Barwaha, Murad, and Napsi (fig. 10.6). These alkaline rocks are denser than the Deccan basalts with clearly defined gravity high, and were emplaced as fluid ejecta in a downrange direction (Chatterjee et al. 2006). They produce a spoke-like pattern fanning over 180° of arc from the center of the crater. Some of these fluid ejecta spires are impressive in size. For example, the buried Napsi structure near the city of Mumbai has a maximum diameter of 45 kilometers and is 12 kilometers high, dwarfing Mount Everest (Negi et al. 1993). Alkali igneous complexes are commonly found as melt sheets associated with several Canadian craters. The generation of impact melt by strong shock waves is a characteristic feature of large impacts. The impact melt ponds outside the crater rim are known in large craters on the Moon, Mars, and Venus.

An anomalously high concentration of iridium has been found in two KT boundary sections of India that lie beyond the Deccan province: the Um Sohryngkew river section of Meghalaya and the Anjar volcano-sedimentary section in Gujarat. The KT boundary layer of Meghalaya is a 1.5-centimeter-thick limonite layer that lies within the Mahadeo Formation about 10 meters below the Mahadeo-Langpur contact. This layer is rich in iridium and osmium. The iridium profile at the KT boundary section of Meghalaya is about 12 parts per billion, ten times higher than the background level (Chatterjee et al. 2006).

The Anjar volcano-sedimentary section in Gujarat consists of nine lava flows and at least four intertrappean beds. The third intertrappean bed, about 6 meters thick, is well known for high concentration of iridium, about 6.5 to 13 parts per billion. The iridium layer of the Anjar section has also yielded concentrations of the high-pressure form of fullerenes (C_{60}) (about 13 parts per billion), which probably formed from the impact of the carbonaceous component of the meteorite. Fullerenes are known from the Sadbury impact structure and from the KT boundary sections of North America, and are considered cosmic signatures for impacts. The concentration of fullerenes in the KT boundary sections in North America is low, about 4 parts per billion. The association of a high concentration of fullerenes with a high iridium concentration in

Figure 10.7. Location of the Shiva crater at the KT boundary time, when Seychelles was part of India. The Shiva impact ejecta layer can be traced at several KT boundary sites around the Deccan volcanic province shown in gray circles. These ejecta sites from west to east are: Anjar, Gujarat; Barmer, Rajasthan; Jabalpur, Madhya Pradesh; Um Sohryngkew, Meghalaya; and Ariyalur, Tamil Nadu. Soon after the Shiva impact, Seychelles began to rift and drift away from India.

the Anjar section is a good indicator of a proximate extraterrestrial impact site such as the Shiva crater.

The association of nanoparticles of magnetic and supramagnetic iron oxide phases with the iridium-rich layer at the KT boundary sections of Meghalaya and Anjar are attributed to a meteorite vapor plume with a cosmic signature. From the KT boundary section of Barmer, Rajasthan, I have discovered a distinctive magnetic glassy spherule layer in the Fategarh Formation, just above the Maastrichtian beds, which probably came from the molten droplets of the vapor plume.

The KT boundary section in Jabalpur represents a 2.7-meter-thick ejecta layer on the upper part of the dinosaur-bearing Lameta Formation and is overlain by the Deccan Traps. The sandy ejecta layer contains relatively large shocked quartz grains that show multiple intersecting sets of shock-induced planar features. The thick ejecta layer at Jabalpur demonstrates the existence of a proximate impact site such as the Shiva crater, from which thick distal ejecta could be emplaced ballistically. Such a thick boundary layer could not be derived as airborne fallout from the very distal Chicxulub impact site.

Two kinds of Shiva ejecta have global strew fields containing basaltic spherules and nickel-rich spinels. Since the target rock of the Shiva impact includes the Deccan basalts, the basaltic spherules recovered from different KT boundary sections at several locations around half the globe must have come from the Shiva impact. The spherules originated as droplets of basaltic rock, shock melted by impact and rapidly cooled in ballistic flight to attain global distribution. The Chicxulub target rock, in contrast to Shiva, does not contain any basaltic layer and could not be the provenance for the global distribution of basaltic spherules.

Nickel-rich spinels, another cosmic signature, have been reported from the KT boundary section of Meghalaya associated with an iridium anomaly. Nickel-rich spinels are considered to be of cosmic origin, derived from the vaporization of meteoritic crust; they are widely distributed in the KT boundary sections of Pacific strew fields that lie along the northeast trajectory of the Shiva ejecta.

Deccan Volcanism

Not everybody believes that impacts killed the dinosaurs and other organisms at the KT boundary. Critics have advanced a volcanic alternative. The end of the Cretaceous was also a time of massive continental flood basalt volcanism, such as the Deccan Traps of India. Some scientists argue forcefully that such cataclysmic Deccan volcanism may have been the main contributing factor for the biotic crisis at the KT boundary (Officer et al. 1987; Hallam 1987; Stanley 1987; Courtillot 1990). These gigantic lava floods erupted when India rode over the Reunion hotspot during its northward journey. The Deccan volcanic province is one of the largest volcanic eruptions in Earth's history and today covers an area of 800,000 square kilometers (about the size of Texas) of west-central India and extends seaward more than 500 kilometers beyond the modern

coastline (fig. 10.7). The original volume of lava extruded about 1.2 million cubic kilometers, which today can be seen as layers of lava flows with the greatest thickness of about 3.5 kilometers along the Western Ghats escarpment (Chenet et al. 2007). Recent radiometric dating suggests that Deccan volcanism occurred in three distinct pulses during a span of 3 million years: the initial pulse of eruption (phase 1) occurred at in the late Maastrichtian base around 67.5 million years ago. The main pulse of volcanism (phase 2) probably erupted very rapidly during a span of 1 million years around 65 million years ago at the KT boundary and accounts for 80% of all traps. The last pulse (phase 3) occurred in the Paleocene period in the Early Danian and ended around 64.5 million years ago (Duncan and Pyle 1988; Vandamme and Courtillot 1992; Chennet et al. 2007). The basalt flows that make up the traps alternate with layers of sediment called intertrappeans, which are rich in fossils of plants, invertebrates, and bones and eggshells of dinosaurs. The alternating stratigraphy of the basalts and intertrappean sediments indicates the intermittent nature of eruptions; sediments and fossils were accumulated during the quiet phase when volcanism stopped.

The proponents of the volcanic model argue that the KT extinction was neither global nor instantaneous, but occurred over an extended period, and their evidence is that different organisms disappeared at different levels at or near the KT boundary. Such a stepwise extinction pattern could best be explained by prolonged emissions of volcanic pollutants. Large amounts of iridium have been discovered to be spewing from the Hawaiian and Reunion volcanoes (Olmez et al. 1986), suggesting that the iridium anomaly at the KT boundary could also have had a volcanic origin. There is no doubt that such a massive volcanic outburst over an extended period would have deleterious environmental consequences. Proponents of the volcanic model claim that many of the supposed impact signatures at the KT boundary layer, such as iridium enrichment, shocked quartz, microspherules, clay mineralogy, and soot particles, could have volcanic explanations. The impact proponents disagree. They point out that Deccan volcanism was not explosive and could not account for the global distribution of the iridium anomaly, tektites, and shocked quartz at the KT boundary layer (Alvarez 1986). Moreover, the gradual extinction pattern seen among some organisms may be an artifact of preservation and poor sampling quality. Signor and Lipps (1982) showed theoretically how a sudden catastrophic extinction would appear to have been gradual in the fossil record if the record was not dense. The Signor-Lipps effect weakens the case for a gradual extinction.

A cause-and-effect connection between impact and Deccan volcanism has been the subject of extensive discussion and speculation. Since the Shiva crater was proximate to the Reunion hotspot that created the vast outpouring of the Deccan lava at the KT boundary, the near-coincidence of timing and space is striking (see fig. 10.7). Some geologists have speculated that a major meteorite impact might have released so much energy that the Earth's mantle below ground zero melted, initiating a period of Deccan volcanism (Alt et al. 1988). In this view, the Shiva impact might have triggered Deccan volcanism, analogous to the lunar maria. But the idea does not work for Deccan eruptions, which began at least 2 million years earlier than the impact event, making a causal link unlikely. However, the Shiva impact was so great as to ring the Earth like a bell and cause numerous quiescent volcanoes to erupt; such an event must have shaken every magma chamber of the Earth and greatly increased Deccan volcanic activity. The combined power of impact and volcanism would have devastating effects on the global biota.

Possible Killing Mechanisms at the KT Boundary

The KT extinction consisted of two separate extinction events, terrestrial and marine. It coincided with twin large impact events, one at Chicxulub, Mexico, and the other at Shiva on the Mumbai offshore Basin of India. Both impacts occurred within the time of Deccan flood basalt volcanism in India during the KT transition. As a result, impacts and Deccan volcanism have been implicated as the killing agents for the demise of the dinosaurs and other organisms at the KT boundary. Here I syn-

thesize the roles of impacts and volcanism to assess the proximate causes of the KT extinction.

My results strengthen the conclusion that global climate and environmental instability preceded the KT boundary time by at least 1 million years, primarily caused by the volatile emissions of the Deccan volcanism. The Chicxulub and Shiva impacts devastated global ecosystems, which were already under critical stress from volcanic pollution. Sedimentology and stratigraphy of the KT boundary layer suggest that the main extinction event was effectively instantaneous, and perhaps lasted as much as a few hundred or thousand years. The temporal match between the ejecta layer and the onset of extinctions lead me to conclude that impacts were probably responsible for the final destruction of the ecosystems, while prolonged Deccan volcanism played crucial roles for the acidification of oceans and collapse of the marine food chain. The abruptness of the dinosaur extinction suggests that the twin bolide impacts were probably the fundamental cause of the dinosaur extinction.

Role of Twin Impacts

Large bolide impacts are catastrophic events because they exert stupendous energy bursts in extremely short time periods—virtually a geological blink of an eye. If both Shiva and Chicxulub were formed simultaneously by the splitting of a large asteroid on a rotating globe, the two places to be most adversely affected were India and Mexico, where bolides landed almost in antipodal positions (Chatterjee and Rudra 1996). Most likely, these twin asteroids came from the Near-Earth Asteroid belt whose orbit brings it into close proximity with the Earth and can cause potential hazards. Of about 9,700 NEAs discovered so far, two large asteroids—Sisyphus (~ 10 kilometers in diameter) and Ganymed (~ 40 kilometers in diameter)—correspond well with the estimated sizes of the Chicxulub and Shiva bolides (Chatterjee et al. 2006) that killed the dinosaurs 65 million years ago. Some of the effects of the twin asteroid impacts at the KT boundary that occurred on the opposite sides of the globe were strongest in the equatorial regions surrounding the impact sites along the Alvarez Impact Belt (fig. 10.8). Terrestrial floras suffered especially high extinction rates in these regions. The twin impacts would have instantly produced devastating shock waves; a searing global heat pulse; catastrophic environmental effects such as extended darkness, cooling, and acid rain, as well as earthquakes of magnitude 13 to 15 on the Richter scale, generating gigantic mega-tsunami waves that propagated in all directions from the point of impact and would flood most shorelines about 100 kilometers inward and destroy coastal life (Chapman 2002). The impacts of two massive bolides may have had profound, hitherto unrecognized geodynamic effects on the history of Earth's crust, which claimed dinosaurs, pterosaurs, plesiosaurs, mosasaurs, rudists, ammonites, and more than 75% of animal and plant species on Earth. The pressure exerted by the Chicxulub impact would have generated more than a 100-million-megaton blast and about 10,000 times that of the entire world's nuclear arsenal at the peak of the Cold War (Grieve 1990; Alvarez 1997); the Shiva impact would have been at least ten times more catastrophic than the Chicxulub, and the combined effects would rock the Earth, trigger biotic catastrophe, and wipe out the dinosaurs and other creatures. The biologic consequences of such huge impacts, which were nearly instantaneous in their globally devastating effects, would have depended on many factors, including the energy of the twin impact events, the type and location of target materials, the size of bolides, and the prevailing ecology. While the greatest damage is obviously at ground zero for a large impact, a very significant portion of the energy from the impact would have been dissipated and devastated the ecosphere—the thin shell of air, water, soils, and surface rocks that nurtures life—and would have triggered the mass extinction. Both Chicxulub and Shiva impacts occurred in shallow seas at the continental margins and immediately lofted vast amounts of ejecta into the atmosphere that would envelop Earth and block the Sun; both have been interpreted as low-angle oblique impacts that would prolong global catastrophes. The trajectory of the Chicxulub bolide should have driven a fiery vapor cloud toward the northeast across the North America and the Atlantic Ocean, whereas the Shiva bolide would

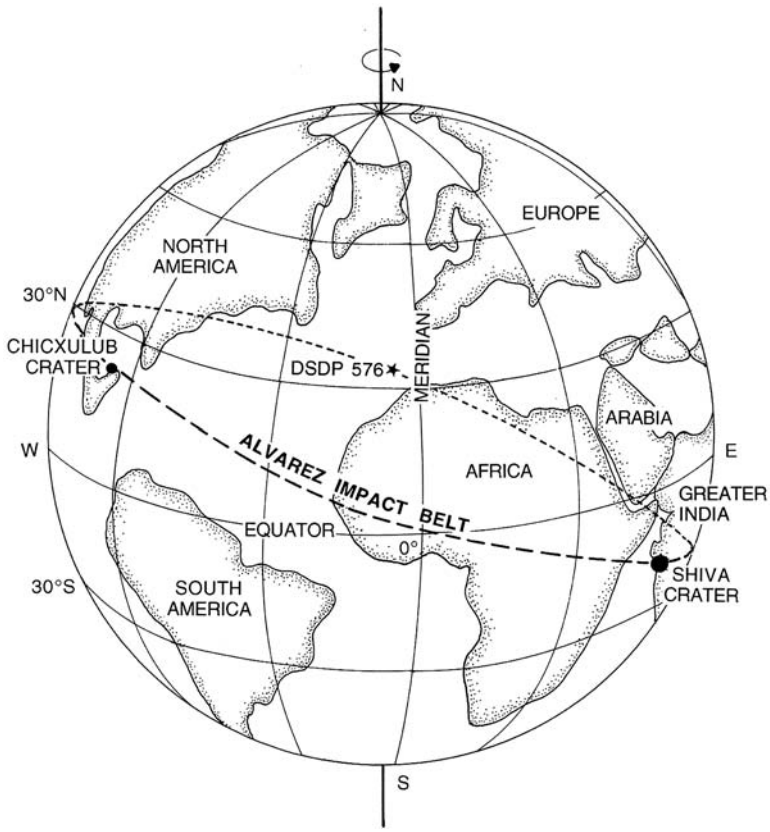


Figure 10.8. Possible genetic links between the Shiva and Chicxulub impact events. Both craters might have originated when two fragments from a large meteorite crashed on a rotating Earth. A tiny fragment of the KT bolide chip and spinel has been found at DSDP 576, indicating that the composition of the asteroid was carbonaceous chondrite.

have created a corridor of incineration in the northeast direction across India and the Pacific Ocean. One of the most destructive forces of the KT extinction was the ignition of vast wildfires that swept across continents (Kring and Dudra 2003). The fires wiped out critical continental habitats and wreaked the base of the food chains. This is evident from the detection of microscopic particles of carbon soot at different KT boundary sections, the ash of the end-Cretaceous event that matches the smoke from forest fires (Wolbach et al. 1988).

When two asteroids hit the Earth in antipodal positions, dust and fireballs that emerged from the craters spread hundreds of kilometers and hid the Sun. Plants and phytoplankton died in prolonged darkness. Some of the killing mechanisms induced by the twin impacts included shock waves, global fires, perpetual night, halt of photosynthesis, collapse of the food chain, ozone layer destruction, toxicity of the environment, acid trauma, nuclear winter, earthquakes, and tsunamis (Alvarez 1997). An infrared thermal pulse from a global rain of hot spherules splashed from the KT impacts could be the one of the prime killing agents (Robertson et al. 2004). According to this model, for several hours following the impacts, the entire Earth was scorched with infrared radiation from reentering ejecta that would have killed unsheltered large animals directly and ignited global fires that consumed Earth's forests and their inhabitants. Smaller species such as mammals and squamates that lived underground or freshwater animals such as turtles and crocodiles would have been least vulnerable to heat and fire. Soot and impact-generated dust choked the sky and blocked the Sun to create perpetual night that halted photosynthesis so that plants and phytoplanktons died and food chains collapsed.

In India, bones and eggshells of dinosaurs such as carnivore abelisaurs and herbivore titanosaurs were found in intertrappean beds of the Deccan Traps, very close to the KT boundary iridium layer, which suggests that the dinosaur extinction was sudden and right at the boundary (Chatterjee and Rudra 1996). Dinosaurs survived the first few phases of Deccan volcanism but disappeared precisely at the KT boundary iridium anomaly at the Anjar section of the Gujarat of western India. The Indian stratigraphic evidence clearly suggests that the dinosaurs did not become extinct well before the KT boundary during the early phase of Deccan eruption, but lived right up to it. The sudden dinosaur extinction in the essentially complete KT boundary section in the Anjar section just below the iridium layer supports the Alvarez model that the KT extinction was a catastrophic event, induced by the impact, not by volcanism.

I collected boundary samples from the Anjar section where associated skeletons of titanosaurs occur for iridium analysis. Dr. Moses Atrrep Jr., of Los Alamos National Laboratory, did the iridium analysis. He detected iridium at 348 parts per billion in the samples—indicating significant enrichment consistent with other KT boundary material. This is the first unequivocal evidence indicating that the dinosaur extinction occurred precisely at the time of the impact. We believe that the main culprit for the KT extinction was the titanic lethal effect generated by the impacts—vapor plumes, global fires, thermal pulses, evaporation of the photic zone and concomitant sea regression, chondritic metal toxicity, acid rain, and volatilization of target rocks. The impacts probably caused more dramatic changes to KT environments globally and a more traumatic crisis to ecosystems than could volcanic emissions. Impacts also perturbed the environment so suddenly and catastrophically that most organisms could not adapt to these changes in such a short time and perished instantly. In contrast, prolonged volcanism allowed enough time for some organisms to adapt and for others to disappear gradually.

Role of Deccan Volcanism

Other than the twin impacts, another agent that affected the Masstrichtian life was Deccan volcanism that erupted in three major pulses for almost 3 million years. Some of the consequences of asteroid impacts and of massive volcanism would be quite similar such as pollution of the atmosphere, darkness resulting from dust (either ejecta or ash), suppression of photosynthesis, acid rain, global climatic changes, carbonate crisis in the ocean waters, environmental stress, devastation of ecosystems, and the collapse of the food chain. However, massive volcanism would lack some of the titanic lethal catastrophe produced by gigantic shock waves of impacts. The long-term hazard of Deccan volcanism would be several trillion tons of toxic gases pumped into the upper atmosphere, which would result in global climatic perturbations disrupting the ecosystem (Chatterjee and Rudra 1996). Based on the data known from the Laki eruption in Iceland in 1783, the Deccan eruption must have pumped large volumes of sulfur dioxide and carbon dioxide, as well as ash particles, into the atmosphere to cause global cooling, immense amounts of acid rain, reduction in the alkalinity and pH of the surface of the ocean, and ozone layer depletion that might be harmful to both terrestrial and marine organisms (Hallam 1987; Keller 2012). The gas emissions from the Deccan eruptions, particularly sulfur dioxide and carbon dioxide, had the most severe kill effect. Both sulfur dioxide and carbon dioxide gases, when mixed with rainwater, create corrosive acid rain of sulfuric acid and carbonic acid that travels from river to ocean and changes the chemistry of seawater from an alkaline to an acidic condition. They also perturb the global climate. Deccan volcanism must have produced large-scale aerosol clouds of sulfur dioxide, which act to reflect incoming solar radiation and cause global cooling, leading to severe environmental consequences. The reduction in temperatures caused by sulfur dioxide aerosols in the stratosphere act in the opposite direction to the greenhouse gases such as carbon dioxide; the former cools the climate, the latter causes global warming. There were chaotic climatic perturbations caused by Deccan pollutants, making it difficult for organisms to adapt to the extreme cold or hot environments. Environmental consequences of the massive Deccan eruptions were likely devastating, with acidification of ocean water and the collapse of the marine biota. Deccan volcanism must

have played a significant role in the initial breakdown of the marine food chain by acidification of seawater, which was detrimental to calcareous organisms. With the emissions of Deccan pollutants, the countdown of disruption of oceanic biota started at least a million years before the KT event.

Since India was ground zero for Deccan volcanism, this would be an ideal place to search for evidence of the crisis on local biota. The vast thickness of the Deccan lava flows were not extruded all at once. Between the lava flows are fluvial or lacustrine deposits of Lameta sediments that contain abundant remains of plants, invertebrates, dinosaurs, and dinosaur eggs. Damming of local drainage by lava flows had created new lakes in subaerial environments. Such lakeshores were centers for dinosaur communities and became their favorite nesting sites. We could not detect any evidence of biotic crisis in these fossil assemblages during episodic volcanic activity. On the contrary, the fossil evidence indicates that dinosaurs were thriving and reproducing during the recurrent Deccan eruptions, quite unaffected by millions of years of volcanic activity (fig. 10.9). Thus the eruption of the Deccan volcanism was not immediately inimical to life, even when the lavas were right next door. Moreover, no bones or eggs from this locality show any pathological abnormality. The extrusion of Deccan volcanism certainly affected the local flora and fauna by habitat destruction and pollution, but it had little direct effect on the major decimation of terrestrial organisms. Deccan volcanism consisted largely of nonexplosive tholeiitic eruptions similar to the Kilauea and Reunion emissions, though on a grander scale. Recurrent eruptions do not disrupt much of the rich biota on the islands of Hawaii and Reunion. The fact that dinosaurs survived on the very site of the eruptions suggests that Deccan volcanism cannot be the proximate cause of the mass extinction. Within the intertrappean beds, magnificent dinosaur fossil accumulations such as abelisaurs and titanosaurs indicate that life was resilient in the hostile environment of Deccan volcanism (Chatterjee and Rudra 1996).

The environmental crisis induced by Deccan volcanic emissions would have been intensified a million times by collision of twin asteroids at the KT boundary. The impact would inject a large volume of dust into the stratosphere, darken the skies, halt photosynthesis, ignite global fires, decrease the alkalinity of the ocean surface, and devastate the biosphere. Millions of organisms would die instantly from the direct effect of the impact—shock heating of the atmosphere by the expanding fireball. Most of the world's vegetation would be caught in wildfire. The fireball would fuse megatons of oxygen and nitrogen of the lower atmosphere to combine with steam, forming nitric acid, turning the alkaline sea to acid. This would have destroyed the myriad of calcareous planktons, collapsing the food chain in the sea. Since the impact occurred at the coastal region, huge tsunamis produced by the impact would destroy shallow marine habitats across the globe. Many tsunami deposits linked to the KT impact have been discovered along the Gulf Coast (Hildebrand et al. 1991) and across India (Chatterjee et al. 2006; Keller 2012). The thick deposits of anhydrite on the coastal regions, when impacted, would have created a huge sulfuric acid aerosol cloud, thereby generating greater environmental stress than would have been possible with impact dust alone. The acid aerosol cloud would contribute to a rapid decline of global surface temperature and halt photosynthesis, heralding a "nuclear winter" and killing most of the plants and animals that survived the initial cataclysm (Sharpton and Ward 1990).

The volcanic model can better explain selectivity and the stepwise extinction pattern in marine organisms. Deccan volcanism could have been an accomplice, but not the main killer, in this massive destruction of life. It seems that impact was the proximate cause of the biotic crisis at the KT boundary, whereas long-term volcanism produced harmful changes that increased the climatic stress and enhanced the extinction process. Both the impacts and Deccan volcanism contributed heavily to the breakdown of stable ecological communities and disrupted the biosphere. The KT extinction was a compound crisis, induced by both impact and volcanism (Silver and Schultz 1982; Sharpton and Ward 1990). It seems that twin impacts at the KT boundary were the final blow

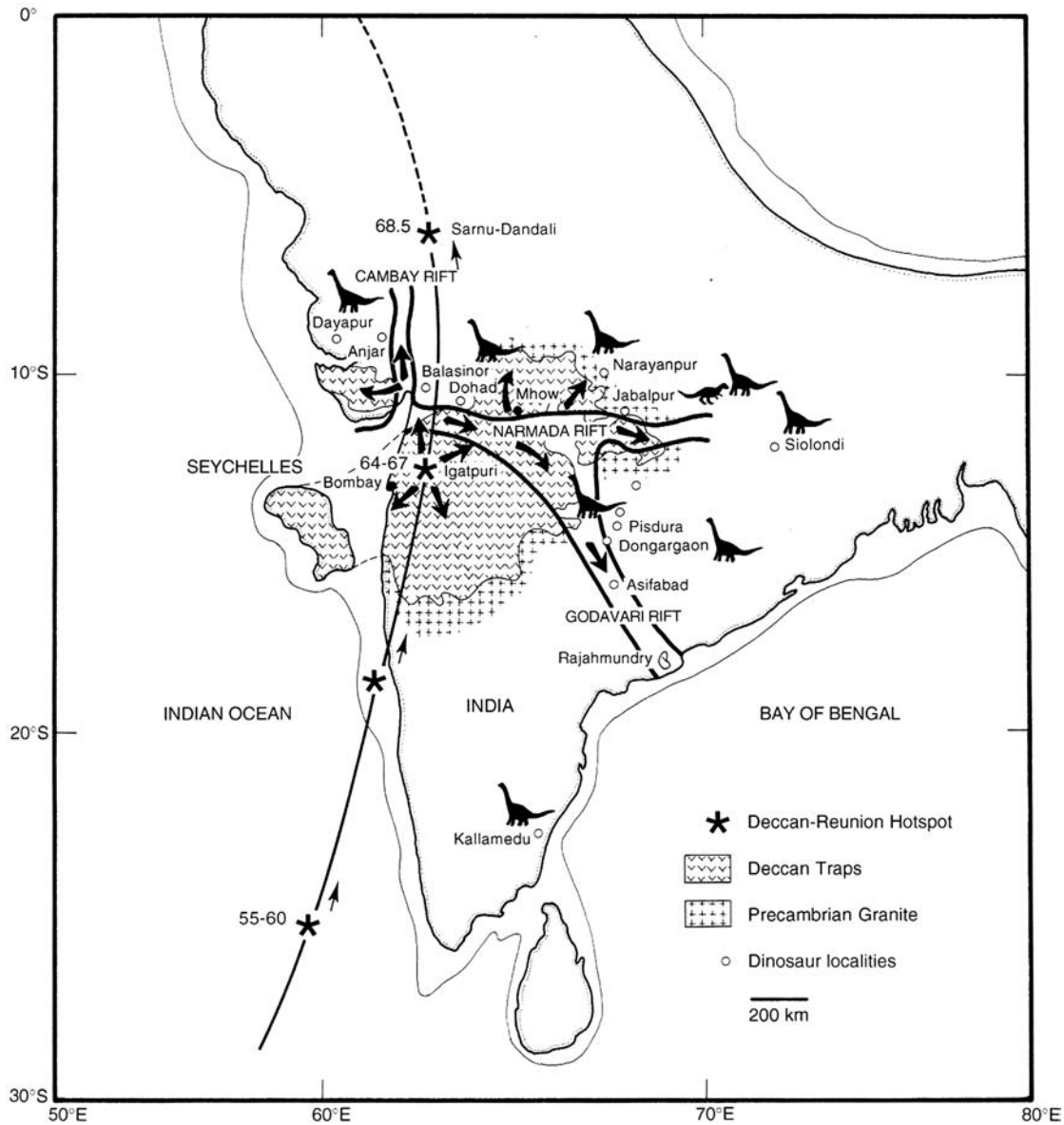


Figure 10.9. Sketch map showing the localities of the Maastrichtian dinosaurs around the Deccan volcanic province. The position of India is reconstructed as it was during the Late Cretaceous period. Dinosaurs were thriving and reproducing when the Deccan lava was erupting, quite unaffected by millions of years of volcanic activity, thus suggesting that the eruptions were not catastrophic.

to the already overstressed global ecosystems initiated by the prolonged period of Deccan volcanism.

Aftermath of the KT Extinction

The KT event is surely the best-known mass extinction because it caused the demise of dinosaurs, but several groups of terrestrial tetrapods such as pterosaurs disappeared, as well as several families of birds and mammals. After fires had ravaged the landscape, the postimpact environment was less diverse. Ferns, shrubs, and algae were first to recover in swamps and at water's edge. Trees began to grow and angiosperm forests began to proliferate. In this new world, some forms of life such as modern birds and placental mammals rebounded. They formerly played minor roles during the final days of dinosaurs, but assumed prominent roles after the extinction. Our

knowledge of avian victims and survivors at the end of the Cretaceous is still sketchy. The primary victims included the various archaic lineages of birds such as Hesperornithes, Ichthyornithes, Enantiornithes, and Palinotropiformes along with other, less well-known groups whose general appearance was quite different from that of extant birds. Longrich et al. (2011) recognized seventeen species of birds from the latest Maastrichtian of western North America that died suddenly at the KT boundary. None of the archaic lineages survived after the KT extinction.

In the beginning of Paleogene, we see the radiation of avian, or modern, birds that flourished in the aftermath of the extinction. Although a wealth of new discoveries has shown that the Cretaceous was a time of active diversification of birds, the record of modern birds in the Cretaceous consists almost entirely of fragmentary and dissociated specimens. Hope (2002) identified several groups of modern birds in the Late Cretaceous sediments from fragmentary remains such as anseriforms, cormorants, and galliforms. The only definitive Aves recognized in the late Maastrichtian is the anseriform *Polarornis* (= *Vegavis*) from Antarctica. At least, duck, chicken, and ratite bird relatives coexisted with nonavians but survived the KT extinction. The mass extinction of archaic birds at the KT boundary opened up an ecologic opportunity for the adaptive radiation of surviving Aves in the Paleogene that quickly filled the niches left vacant by pterosaurs. This pattern of radiation has been referred to as the "explosive evolution" of modern birds, which was proceeded by two early stages of macroevolution, an "origin" and a "phylogenetic fuse" in the Late Cretaceous (see the following chapter).

Throughout the Mesozoic both birds and pterosaurs competed for aerial niches but adapted to different habitats. Pterosaurs were a successful group of reptiles that appeared at the dawn of the age of dinosaurs, flourished throughout the Mesozoic, and then disappeared at the end of the Cretaceous. Most of the Maastrichtian pterosaurs became large and relied heavily on sea breezes and thermals for soaring and gliding. They had poor terrestrial ability and occupied relatively narrow ecological niches along cliffs in warm, near-shore marine environments, where their diet relied heavily on fish and other sea creatures. In contrast, Cretaceous birds were relatively small, had adapted to a wide range of habitats in both terrestrial and marine realms, and had ecological superiority over pterosaurs. Their small size and versatile lifestyles may have enhanced survival during the crisis. Unwin (1988) pointed out that during the Late Cretaceous, as bird diversity rose, that of the pterosaurs steadily declined. The success of birds over pterosaurs at the end of the Cretaceous may be linked to differential survival strategy. Large-bodied pterosaurs had two disadvantages: they generally had smaller populations and lower reproductive rates than smaller-bodied bird species. When struck by catastrophe, they were slower to recover. In contrast, birds, being small, were able to reproduce quickly and expand their numbers. They endured massive extinction at the end of the Cretaceous but rebounded from this crisis and underwent an explosive radiation of modern forms in the Tertiary. The dinosaur heritage of modern birds, however, cannot be ignored. The pinnacle of dinosaur evolution may have culminated in the ascendancy of birds. "There is a grandeur in this view of life" (Darwin, 1859, 437) that dinosaurs did not completely vanish from the Earth after the Cretaceous catastrophe. The sole surviving lineage of dinosaurs is still around us—we call them *birds* (Bakker 1975).

11 The Avian Revolution Begins

From the ashes a fire shall be woken,
A light from the shadows shall spring;
Renewed shall be blade that was broken:
The crownless again shall be king.

J.R.R. Tolkien, *The Lord of the Rings*, 1965

The end-Cretaceous mass extinction left an impoverished fauna on the land with the disappearance of nonavian dinosaurs, but an evolutionary rebound during the Early Tertiary once again brought back biodiversity. The Cretaceous crisis was an important component in the evolution and shaping of Tertiary life. The demise of pterosaurs left vast airspaces devoid of flying vertebrates, and vacant spaces were soon occupied by newly evolving and diversifying modern birds. At least three groups of modern birds—palaeognaths, galliforms, and anseriforms—transcended the KT extinction and continued into the Cenozoic. From this evolutionary bottleneck, birds underwent an explosive evolution in the beginning of the Tertiary, diversifying and adapting to many different ecological niches.

The KT extinction created opportunities for faunal change by removing nonavian dinosaurs from the land and pterosaurs from the sky and enabling mammals and birds to radiate and multiply in vacant niches. The extinction was like the cosmic dance of the Hindu god Shiva, who holds in his left hand the final all-consuming flames of destruction pronouncing the end, and in his right, a drum, whose sound is the sound of creation, which thus heralds a new beginning. Shiva is the god not only of destruction. He also creates a new world out of the wreckage of the old. In the Early Tertiary, this new world began with the rise of mammals and birds. Both groups flourished and blossomed into a myriad of new species in the aftermath of the extinction. The success of birds in the Tertiary was critically linked to the disappearance of pterosaurs in the same way that the success of mammals was linked to the destruction of dinosaurs. Today, birds are certainly highly prolific vertebrates, sharing with the mammals a long evolutionary history, species diversity, endothermic physiology, and a wide range of dietary habits.

Avian Ascendancy in the Cenozoic

The rise of modern birds in the Cenozoic era is phenomenal (fig. 11.1). By the beginning of Cenozoic times, birds had acquired their present sophisticated body plan. The Cenozoic was a renaissance—a time of peak radiation of bird types, when as many as six-

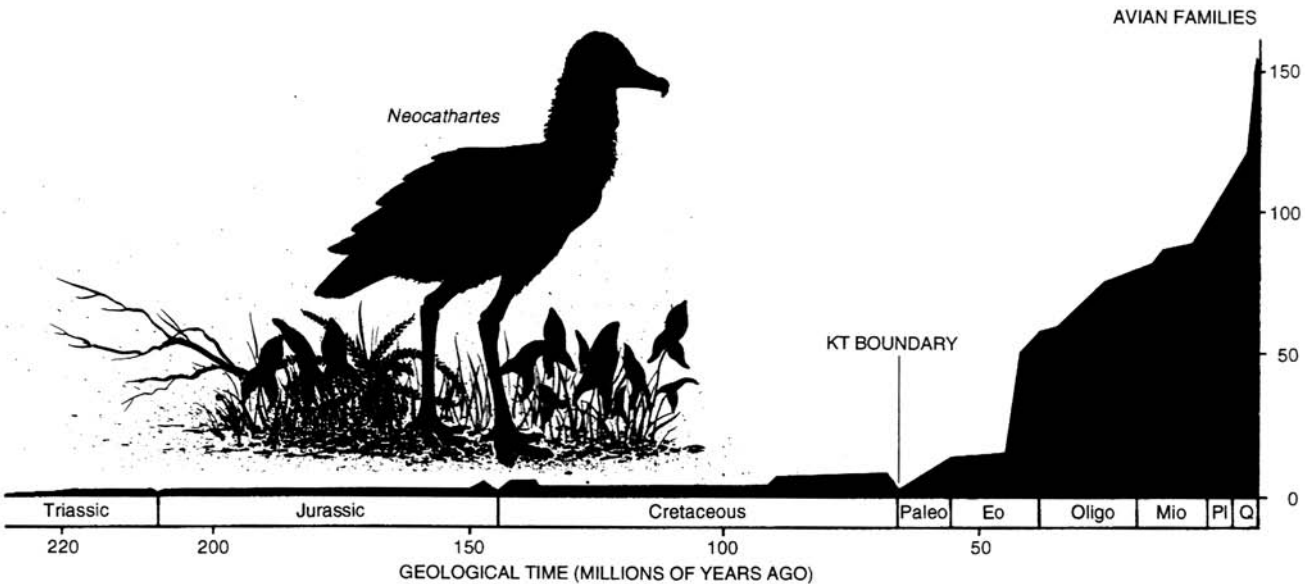


Figure 11.1. Graph charting the rise in avian diversity. Note the pattern of explosive evolution of birds after the KT extinction (modified from Unwin 1988). Inset, *Neocathartes*, a scavenging bird from the Eocene of Wyoming, was a forerunner of the New World vulture of today. Paleo, Paleocene; Eo, Eocene; Oligo, Oligocene; Mio, Miocene; Pl, Pliocene; Q, Quaternary (after Chatterjee 1997).

teen new orders developed worldwide. The Paleocene-Eocene world, a period of less than 15 million years, was warm, had almost subtropical climates from pole to equator, and supported a great diversity of birds. These birds are generally structural intermediates to modern families and occupied quite different niches from those of their living descendants. Many of these early birds show telltale signs of their modern descendants.

Our knowledge of the Paleocene birds is limited; most records come from France and Mongolia. The French fauna contains the gigantic flightless bird *Gastrornis,* an early ratite, and a wide variety of owls. The oldest owl fossil, *Ogygoptynx*, is known from the Paleocene of Colorado. The most striking event in early Cenozoic avian history was the rapid radiation of large, flightless, cursorial birds, which invaded the ecological niches left by the extinct nonavian dinosaurs. Such ecological replacement is an example of evolutionary relay. During this period mammals were generally small and birds made a brief bid for supremacy. Flightlessness has evolved in many lineages of fossil and modern groups, often associated with geographic isolation and the relative absence of predators. During the Early Tertiary, large, flightless, cursorial birds were widely distributed globally in the expansive open plains. They evolved convergently from different stocks and disappeared at different times. Among these flightless forms, we see the radiation of both carnivores and herbivores.

Probably the most impressive birds to inhabit the Paleocene-Eocene landscape of the Northern Hemisphere were the giant diatrymas (*Diatryma*, *Gastrornis*, and related forms). Their remains have been found in Wyoming, New Mexico, New Jersey, France, and Germany. Diatrymas were large birds, standing more than 2 meters tall and weighing perhaps 190 kilograms. They had a huge head, an enormous beak, vestigial wings, and long, powerful legs (fig. 11.2A). Against the widespread view of diatrymas as cursorial predators, Andors (1995) offered a novel interpretation of their mode of life. He suggested that these birds were largely herbivores, similar to the living takahe of New Zealand, and were related to anseriform birds.

In South America, the formidable phorusrhacids were the dominant carnivores throughout the Tertiary and assumed the role of theropods (Marshall 1994). They were first known from the Paleocene of Brazil. During this time South America was geographically isolated from North

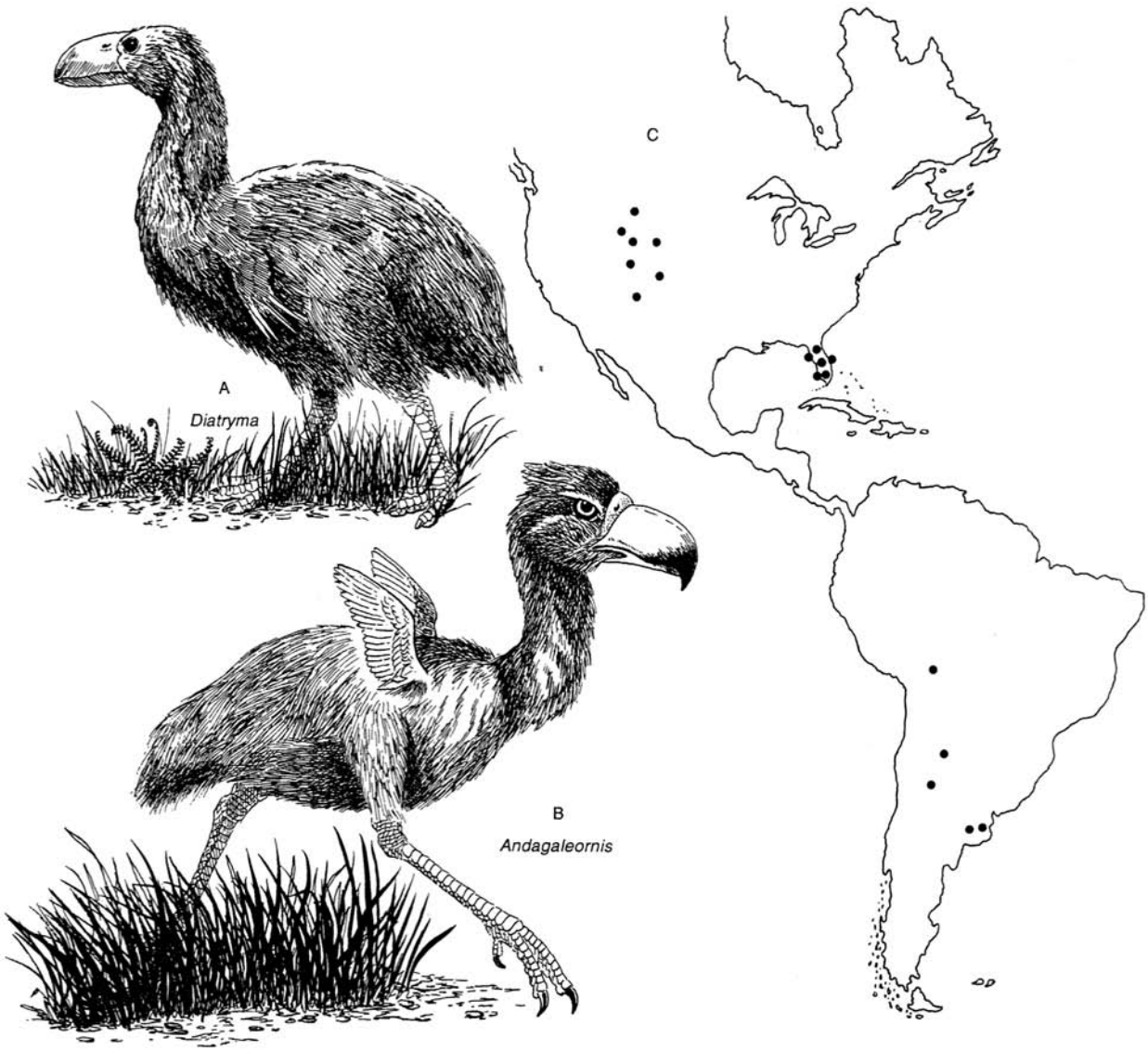


Figure 11.2. Restorations of giant flightless birds of the Tertiary period. A, the flightless, herbivorous groundbird *Diatryma*, known from the Eocene of the western United States and Europe. B, the terror bird phorusrhacid *Andagaleornis* of the Pliocene of South America. C, distributions of diatrymas in North America and of phorusrhacids in South America (after Chatterjee 1997).

America and lacked large predatory mammals. Geographic isolation and lack of competition favored the dominance of phorusrhacids. These giant birds were lightly built and about 1.5 meters tall, with a powerful hooked beak highly adapted for tearing flesh and crushing bone (fig. 11.2B). Living on the pampas, these birds must have terrorized the diminutive mammals of the time. The decline of these predatory birds began some 2.5 million years ago, when the placental carnivores invaded their range from North America. Phorusrhacids are also known from the Eocene deposits of Europe and the Antarctic Peninsula. The seriemas of South America represent the living relatives of phorusrhacids.

The superiority of large flightless birds in the Early Tertiary period was short-lived. With the passage of time, there was active competition between flightless birds and mammals for the role of dominant land vertebrates. Mammals won the contest because of the variety and efficiency

of their teeth, with designs for cutting, shearing, piercing, gnawing, grinding, grasping, and processing food. The evolution of precise food-processing mechanisms played a crucial part in mammals' supremacy over ground birds. Many ground birds were unable to protect their chicks, hatched on the ground, from small, fast, predatory mammals. From then on, birds largely became flying vertebrates and avoided direct confrontation with mammals for food and resources. By the Eocene most modern orders of nonpasserine birds had appeared. During this time, shorebirds, flamingo-like birds, and crane- and rail-like forms were extremely diverse. Many of these birds are structural intermediates and provide evolutionary links between modern families.

There are spectacular bird fossils from the Early Eocene Green River Formation of Wyoming and London Clay of England, the Middle Eocene Oil Shales of Messel, Germany, and the Eocene-Oligocene phosphorite deposits of Quercy, France. The Green River sediments were deposited in three lake basins of Wyoming and Utah, such as Lake Uinta, Lake Gosiute, and Fossil Lake, under tropical climates during the orogeny of the Rocky Mountains. These fine-grained lake sediments have produced a rich array of avian fauna, such as the frigate bird *Limnofregata*; the galliform *Gallinuloides*; the perching birds *Primobucco* and *Neanis*; *Presbyornis,* a transitional bird between duck and flamingo; several undescribed species of coraciiforms and caprimulgiforms; as well as feathers and footprints (fig. 11.3). These specimens are represented by complete or nearly complete articulated skeletons. Many of these birds were nonaquatic, fell accidentally into alkaline lakes, like those found in the Rift Valley of Africa, and were preserved in exquisite detail (Grande 1980; Feduccia 1980). Several raptors were also recorded during this period; the most famous is *Neocathartes*, a long-legged, terrestrial vulturine bird that scavenged along the shores of large inland lakes (fig. 11.1).

The Messel Oil Shale bed near Frankfurt, Germany, is another famous site for Middle Eocene flora and fauna, designated as a World Heritage Site, preserved for the extraordinary richness and quality of its fossil remains. During the Middle Eocene, Europe was an island that lay 10° latitude farther south than it does today. The Messel setting was a rainforest environment around a lake, where many species of birds lived in bushes or trees and died accidentally in the lakebeds along with a vast number of other animals. The deposits preserve a maar lake, a flooded volcanic crater, and fossils suggestive of a wide range of habitats. The Messel shale has yielded excellent articulated skeletons of birds, often with soft tissue preservation, with great evolutionary significance (fig. 11.4). The Messel birds include representatives of both extinct and extant groups, ranging in size from the tiny *Messelirrisor* with a wingspan of 17 centimeters to flightless giants such as *Diatryma*, some 1.7 meters tall. These spectacular groundbirds include the ancestral ratite *Palaeotis*, diatrymas, phorusrhacoids, and seriemas. Other forms include hawks, galliforms, ibises, rails, plovers, owls, swifts, woodpeckers, and rollers. Occasionally, feathers are found preserved. Surprisingly, typical aquatic birds are rare in or absent from the Messel assemblage, except for the stilt-like *Juncitarsus*, which sheds new light on the origin of flamingos (Peters 1992, 1995).

The extensive terrestrial avifauna of the phosphorites of Quercy, France, includes galliforms (*Paraortyx*, *Palaeocryptonyx*, *Priotryx*, and *Palaeotyx*), gruiforms (*Idiornis* and *Elaphrocnemus*), the caprimulgiform *Aegialornis*, and the trogon-like *Archaeotrogon* (Mourer-Chauviré 1992). Large seabirds with tooth-like projections on the jaws, such as *Odontopteryx*, and pelecaniforms like *Prophaethon* were known from the London clay deposits. Odontopterygiformes were albatross-like birds, essentially fish-eaters, which survived until the Pliocene. The penguins are a very ancient order; their earliest fossils have been found from the Late Eocene of the Antarctic Peninsula.

During this period worldwide cooling began, when global temperatures dropped as much as 10°C. This is the beginning of the explosive radiation of birds. By this time they had acquired their basic forms as fliers, swimmers, and runners. The earliest known passerines (altricial songbirds of perching habits) come from the Oligocene deposits of France. The Oligocene period brought further progress toward recent forms of bird life. Nearly all families of nonpasserines may have existed at this time.

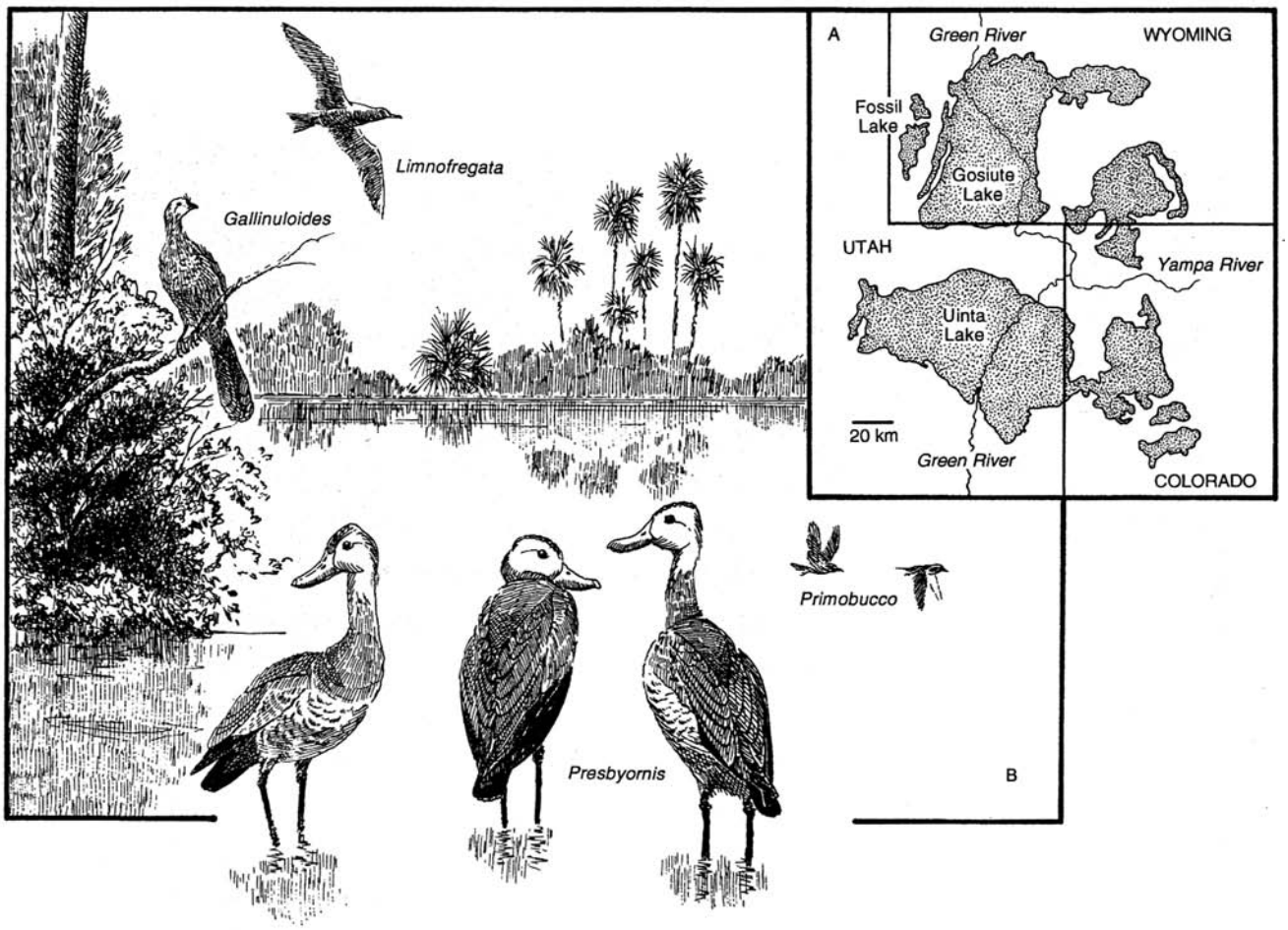


Figure 11.3. Green River bird assemblages of the Eocene epoch. A, surface exposures of the Eocene Green River Formation (simplified from Grande 1980). B, reconstruction of the Green River avian community showing *Presbyornis*, *Gallinuloides*, *Limnofregata*, and *Primobucco*, which lived in and around large lakes (after Chatterjee 1997).

There were grebes, flamingos, albatrosses, cranes, limpkins, rails, woodpeckers, hawks, eagles, and vultures. The Early Miocene was marked by slight warming, but by the Middle Miocene Antarctica was covered by an ice sheet. The global climate began to cool and become much drier, leading to the widespread growth of grassy savannas. During this time, the majority of avian families and many genera of contemporary birds appeared. The Miocene avifauna is extremely rich. Various passerine birds, such as crows, thrushes, wagtails, shrikes, and wood warblers, also evolved. A giant pelecaniform bird, *Osteodontornis*, with jaws containing tooth-like bony projections, is also known from the Miocene of California. The largest known flying bird, *Argentavis magnificens*, a member of the extinct family Teratornithidae, was also recorded from the Late Miocene deposits of Argentina. *Argentavis* had a wingspan of about 8 meters and stood about 2 meters tall (fig. 11.5). Using a computer simulation model, we calculated the flight performance of *Argentavis* with an estimated mass of 70 kilograms (Chatterjee et al. 2007b). It was probably too large to be capable of continuous flapping flight or standing takeoff under its own muscle power. Like extant condors and vultures, *Argentavis* would have extracted energy from the atmosphere for flight, relying on thermals present on Argentinean pampas to provide power for soaring. Cranial morphology indicates that *Argentavis* was a formidable predator. It could remain airborne during the day while searching for prey over

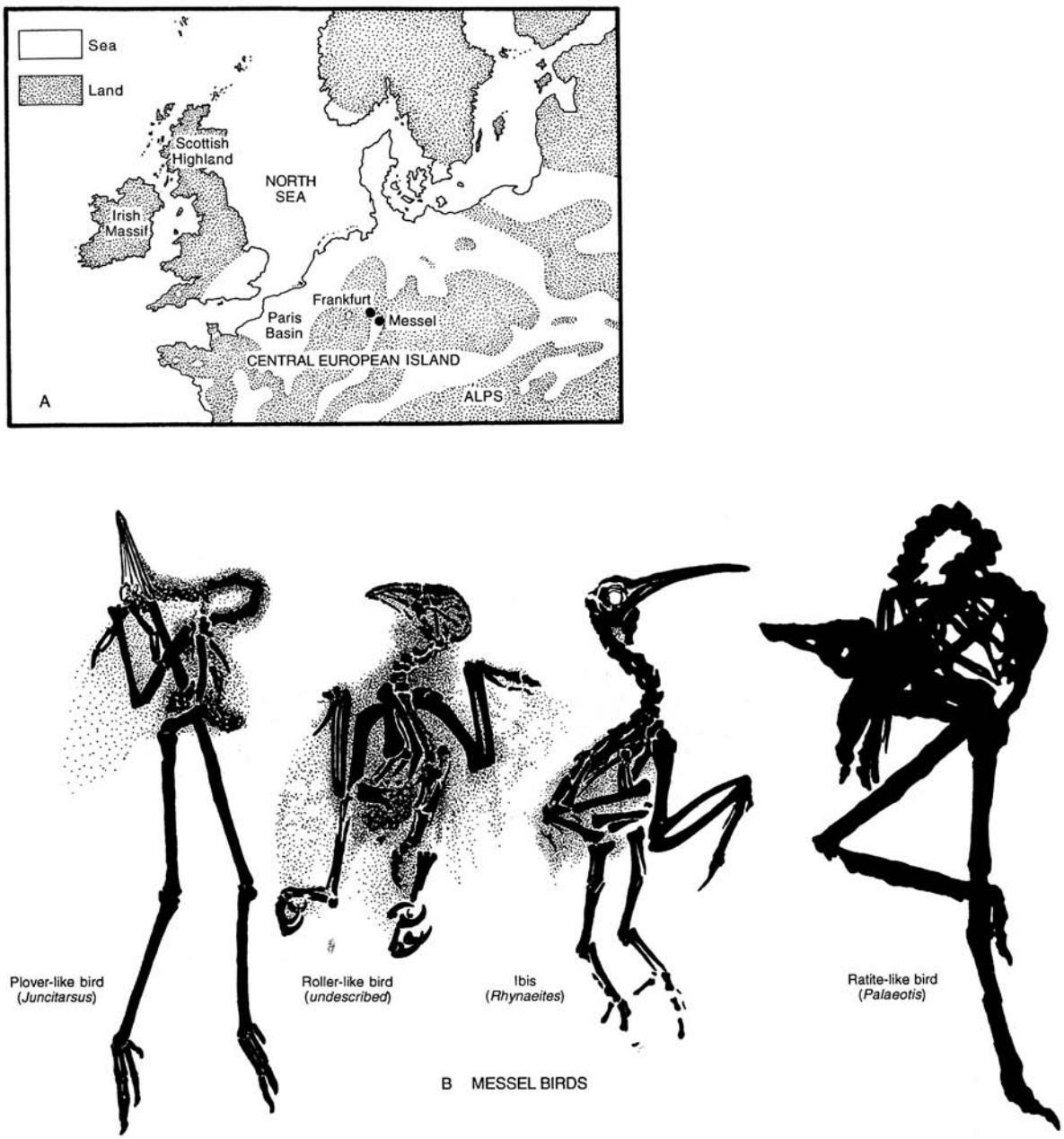


Figure 11.4. Messel bird assemblages of the Eocene epoch. A, Central Europe in the Eocene epoch showing the Messel fossil locality, near Frankfurt, Germany. B, some Messel birds—the plover-like *Juncitarsus*, an unnamed roller, the ibis *Rhynaeites*, and the ratite-like *Palaeotis*—preserved in the Messel shale (after Chatterjee 1997).

the vast open expanses of the pampas. It probably used slope soaring over the windward slopes of the Andes. It was an excellent glider, with a gliding angle close to 3° and a cruising speed of 67 kilometers/hour. *Argentavis* could take off by running downhill like modern albatrosses, or by launching from a perch to pick up flight speed.

In the Pliocene, cooling climates dominated the Northern Hemisphere. An extremely rich avian assemblage is known from South Africa. The spread of savannas favored the appearance of many ground birds, such as ostriches, tinamous, and goatsuckers. The flightless auks and many families of passerine birds are known from this epoch. By

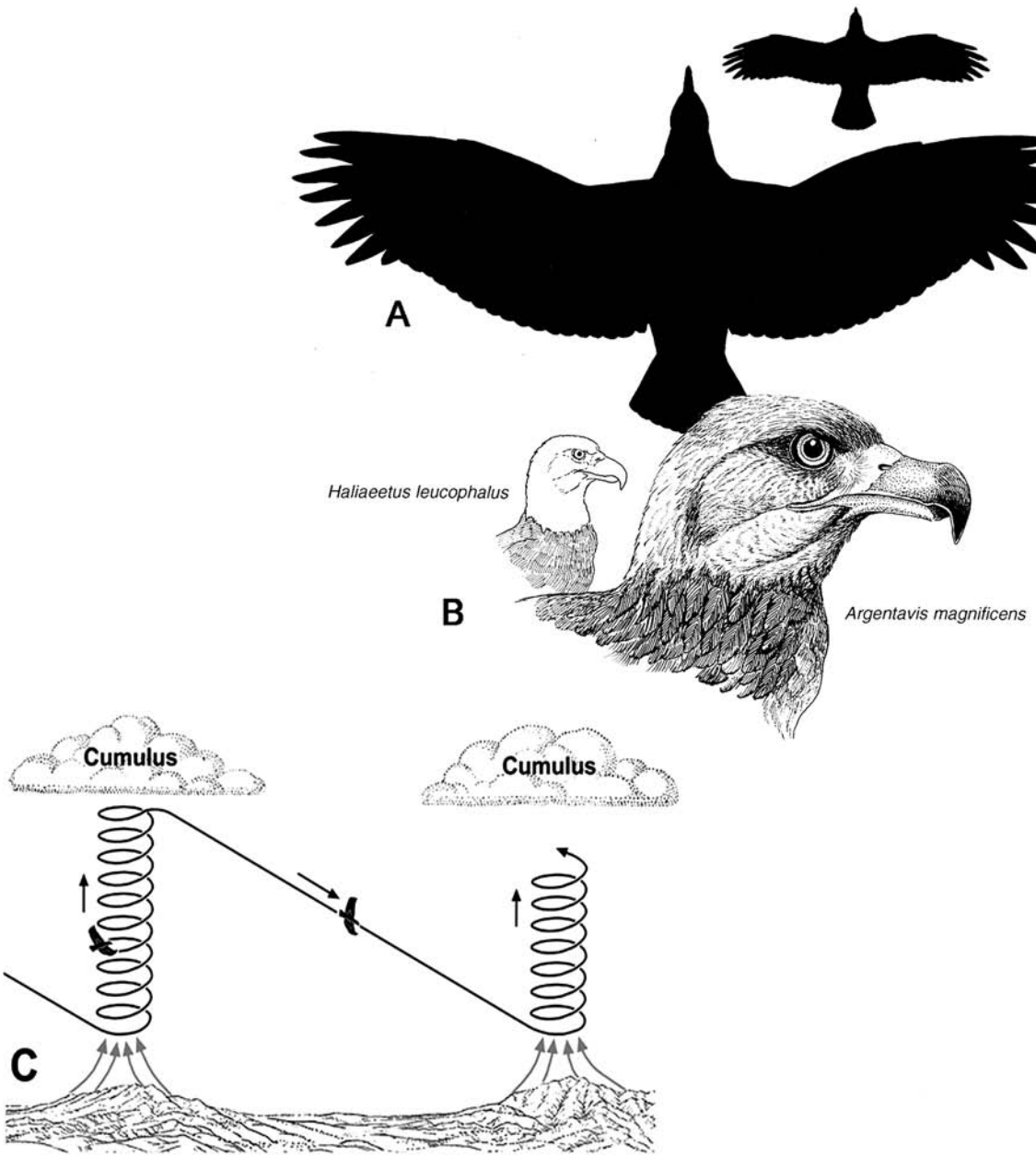


Figure 11.5. The largest known flying bird, *Argentavis magnificens*, with a wingspan of 7 meters, lived in Argentina during the Upper Miocene period, about 6 million years ago. A, the sheer scale of this giant condor is demonstrated by comparing its dorsal wing profile in silhouette with that of the bald eagle (*Haliaeetus leucocephalus*) of today. B, reconstructed head of *Argentavis* is compared with that of the bald eagle for scaling (after Chatterjee 1997). C, many landbirds soar by circling in thermals that require climbing successive thermals and gliding in the desired direction. It is likely that *Argentavis* also exploited thermals for cross-country flight in the Argentinean pampas (after Chatterjee 1997; Chatterjee et al. 2007).

the mid-Pliocene, the Arctic icecap had formed, heralding an ice age. The end of the Pliocene established essentially all modern bird genera.

The Pleistocene record is extremely rich; all recent types had evolved and become established. The Pleistocene was also a period of expansion of many flightless species, including emus, cassowaries, moas, and elephant birds in the southern landmasses. The climate throughout this time continued its deterioration, culminating in the ice ages of the Pleistocene. The connection between North and South America was established, allowing a great interchange of fauna. The flightless, carnivorous groundbird *Titanis* moved from South to North America. In the Northern Hemisphere, the Pleistocene icecaps covered much of the continents.

The most remarkable Ice Age avifauna is known from the Rancho La Brea tar pits of California, where more than 135 species of birds were preserved between 4,000 and 40,000 years ago. Many of these birds represent predatory species, such as falcons, eagles, condors, and vultures, which were probably also carrion-feeders and may have been accidentally caught in the asphalt while attempting to feed on trapped mammals (see fig. 16.3). The largest bird from these deposits, *Teratornis*, which is related to storks and New World vultures, had a wingspan of more than 3 meters. Teratorns were ground-stalking birds as well as opportunist scavengers.

During the Pleistocene glaciation, a large number of avian species suffered extinction. The rapid rise of the Himalayan-Alpine range formed an orographic barrier for bird migration and dramatically altered the climate of Eurasia. Bird life as we know it today was essentially established some 20,000 to 50,000 years ago. The dominant order today is the Passeriformes, which outnumbers all other orders combined.

Phylogeny and Classification of Aves

The taxon name Aves is currently used for several different nested clades of theropods across the phylogeny from the *Archaeopteryx* node to the crown clade of dinosaurs—the modern birds—and is taxonomically confusing. In the dinosaur crown group classification, the taxon name Aves is restricted to the clade that includes the most recent common ancestors of all living bird species and all their descendants with a temporal range from the Late Cretaceous to Recent (Gauthier 1986; Gauthier and de Queiroz 2001). In this definition, the taxon Aves becomes synonymous and interchangeable with the taxon Neornithes. Many authors have preferred the name Neornithes for the crown clade of dinosaurs (Cracraft 1986; Sereno and Rao 1992; Chiappe 1995a, 2007). Thus modern birds have been designated as Aves or Neornithes, often interchangeably. To minimize nomenclatural ambiguity, here I use the name Aves Linnaeus 1758 for the crown clade of birds, which has a priority over the name Neornithes Gadow 1892. Neornithes become a junior synonym of Aves.

The phylogeny and classification of Aves, or modern birds, have captured the interest of ornithologists for more than two centuries. Birds come in all shapes and sizes. The smallest living form, the bee hummingbird of Cuba, is 6.3 centimeters long and weighs less than 3 grams. The ostrich, the largest living bird, may stand 2.5 meters tall and weigh 135 kilograms. Some extinct birds, such as moas and elephant birds, were even larger and may have reached more than 3 meters in height. A Pliocene condor-like bird, *Argentavis,* had an estimated wingspan of 8 meters and was by far the largest known flying bird (fig. 11.5).

Out of this stunning diversity, systematists have tried to classify birds in a meaningful order. The classification of birds should closely reflect their evolutionary history, or phylogeny. Earlier classifications were based on similarity of body structures alone, without regard to phylogeny. Today, however, the central activity of systematic biology is to determine the branching pattern of evolutionary history, called cladistics, as discussed earlier (see chapter 3). All modern birds can be placed in a monophyletic clade, Aves. Avian taxonomy at the species level is well known, but classification at higher levels is in an unsatisfactory state. Our knowledge of the phylogenetic relationships among orders, suborders, and families of birds is inferior to that of mammals and reptiles. Birds are often classified on the basis of external characters like

size, color, and pattern and on habitat. However, many such groupings are the result of convergent evolution from different parental stocks. The taxonomic characters that in other vertebrates would be used for lower-level identification are accorded ordinal rank in the classification of birds. The systematic positions of several bird groups remain open to question.

The Aves includes some ten thousand living species, but at the height of diversity in the Pleistocene period a few thousand years ago, it accommodated more than twelve thousand species. Currently living birds (Aves) are grouped into twenty-seven orders on the basis of evolutionary systematics, but the hierarchical arrangements of taxa within orders and their interrelationships are poorly understood. Recently, there has been an attempt to present a phylogenetic classification of birds that reflects their genealogy and natural hierarchy, based on morphology (Cracraft 1974, 1981, 1988; Mayr and Clarke 2003; Livezey and Zusi 2007) and molecular phylogeny (Sibley and Ahlquist 1990; Sibley and Monroe 1990; Dyke and Van Tuinen 2004; Hackett et al. 2008). Deep avian evolutionary relationships have been difficult to resolve as a result of the explosive radiation of modern birds soon after the KT extinction. Only two nodes at the base of the avian tree are consistently supported by both molecular and morphological phylogenetic studies. The first divides Aves into two lineages: the Palaeognathae (ratites and tinamous) and the Neognathae (all other birds) (fig. 11.6). The second splits the neognaths between the Galloanserae (chickens, ducks, and allies) and the Neoaves (other neognaths). The evolutionary relationships of Neoaves are the most contentious issue in avian phylogeny. Here we attempt to reconcile the molecular and morphologic data to propose a classification of modern birds, linking them to other well-defined groups that reveal their evolutionary history.

Morphological Systematics

The German anatomist Hans Friedrich Gadow (1893) proposed the most comprehensive classification of living birds more than a century ago on the basis of morphological characters. Gadow used forty characters to develop his classification. He used several synapomorphies—palatal conformation, the exact formulation of the leg muscles, the configuration of the internal and external nares, the shape of the toe bones, the presence or absence of a fifth secondary feather, and the exact arrangement of scutes and scales on the legs—to group species into different hierarchical ranks. Although Gadow's classification has been modified and refined by several ornithologists over the years, it still forms the foundation for the morphological classification of birds. Cracraft (1974, 1981, 1988) provided a phylogenetic hypothesis covering the nineteen living orders of neognaths on the basis of morphological evidence (fig. 11.7). Recent phylogenetic analyses of modern birds using large datasets of morphological characters have strengthened the relationships of modern birds (Mayr and Clarke 2003; Clarke et al. 2005; Livezey and Zusi 2007; Dyke and Van Tuinen 2004; Cracraft and Donoghue 2004).

Molecular Systematics

Various attempts have been made in recent years to establish the phylogeny of avian birds using both molecular and morphological evidence, but there is no consensus among researchers. The biomolecular tapestry of Sibley and Ahlquist (1990) was the first attempt to use genetic material (nuclear DNA) as the basis for classification of Neornithes (Aves). They used the DNA-DNA hybridization technique to propose a molecular classification of birds. In this classification, the deoxyribonucleic acid (DNA) of one bird species is compared with that of other birds on the basis of sequence data or genetic distance, and the birds are then grouped accordingly. This classification rests on a simple assumption: once two species separate in evolution, the DNA in the two lines accumulates changes or mutations. By measuring the genetic difference, the length of time since the divergence of two species can be estimated and the relationships between them can be established. Sibley and Ahlquist's (1990) DNA-DNA hybridization analysis was a watershed in the phylogeny of modern birds and inspired subsequent molecular studies (fig. 11.8).

Current molecular analyses focus on mitochondrial or

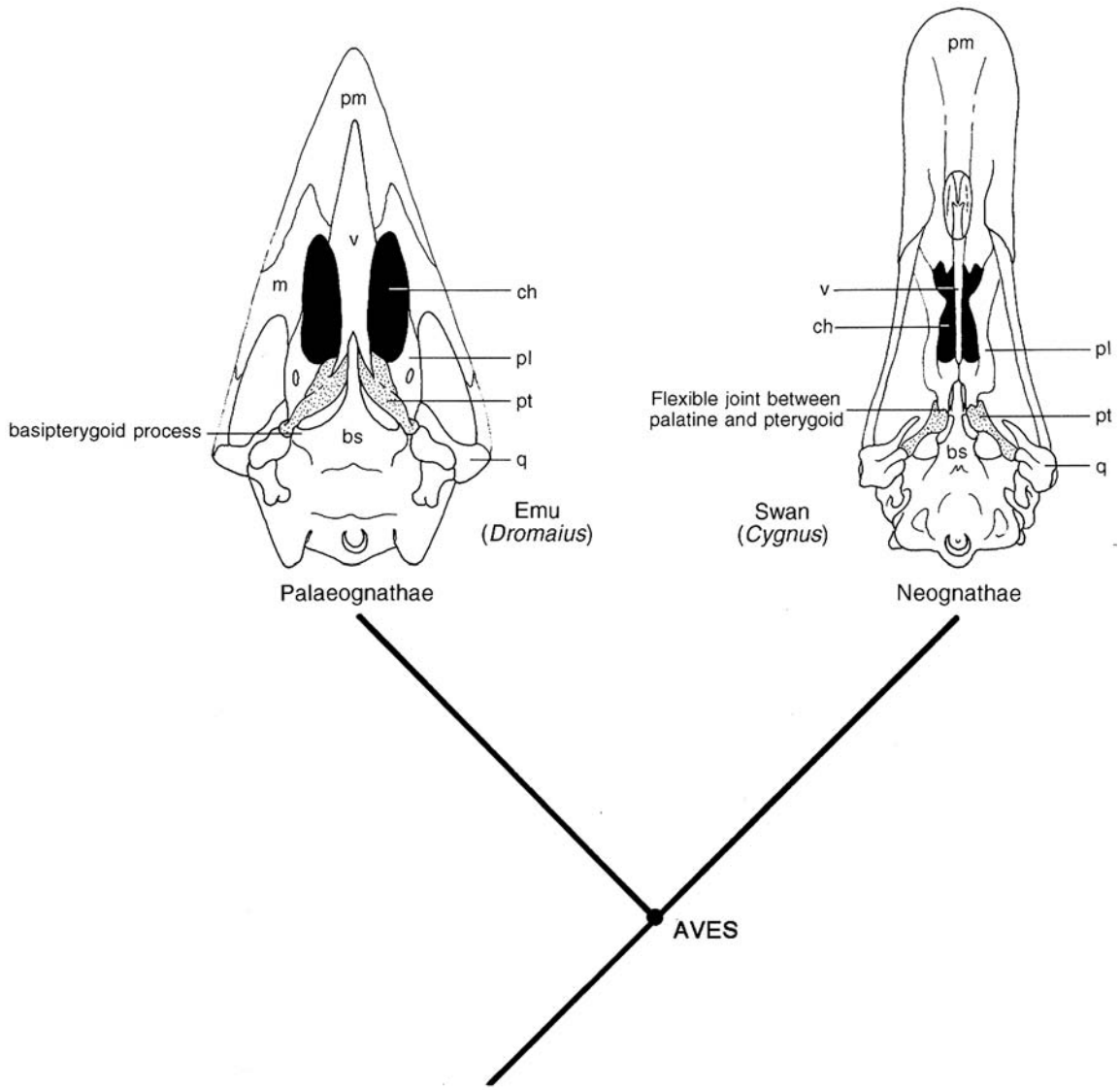


Figure 11.6. Cladogram showing the basal dichotomy of the Aves into Palaeognathae and Neognathae on the basis of palatal structure. Reduction of the vomer and basipterygoid process and development of the flexible joint between the pterygoid and the palatine are novelties for the neognaths. bs, basisphenoid; ch, choana; m, maxilla; pl, palatine; pm, premaxilla; pt, pterygoid; q, quadrate; v, vomer (after Chatterjee 1997)

nuclear gene sequences. In some cases, molecular classification is congruent with the traditional morphological approach. In other cases, however, there is serious discordance between the two methods. One of the unusual results of biochemical classification is the new composition of the order Ciconiiformes, which now incorporates these former orders: Sphenesciformes, Gaviiformes, Podicipediformes, Procellariformes, Charadriiformes, Falconiformes, and Pelecaniformes. One of the reasons for the conflict between morphological and molecular classifications may be the failure to recognize convergences. Since birds have had a single evolutionary history or phylogeny, a compromise between the morphological and biochemical classifications is likely to emerge in the future as data are obtained and critically examined.

In contrast to considerable uncertainties that exist

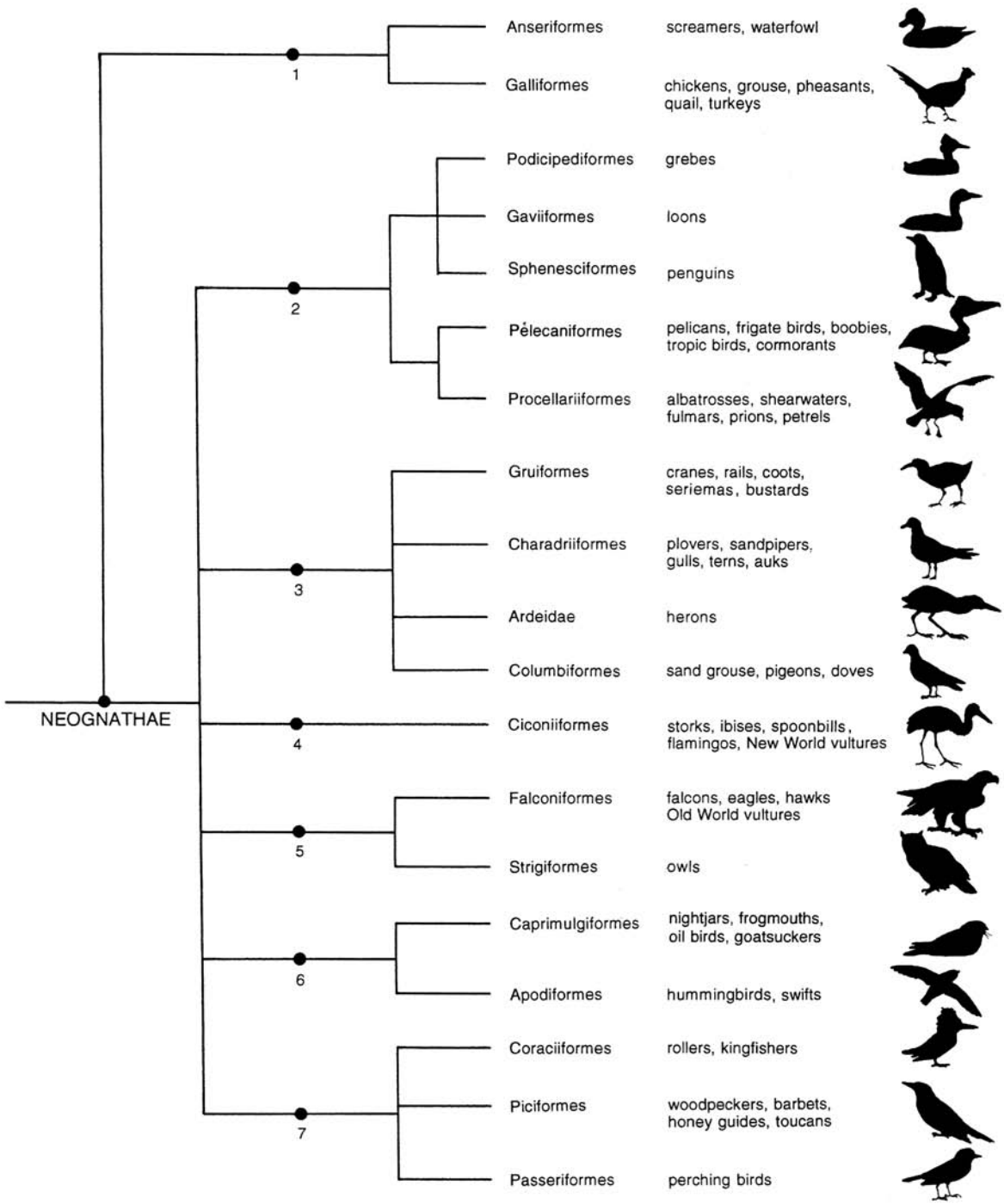


Figure 11.7. Morphological classification of neognathous birds, or Aves (based on data in Cracraft 1986).

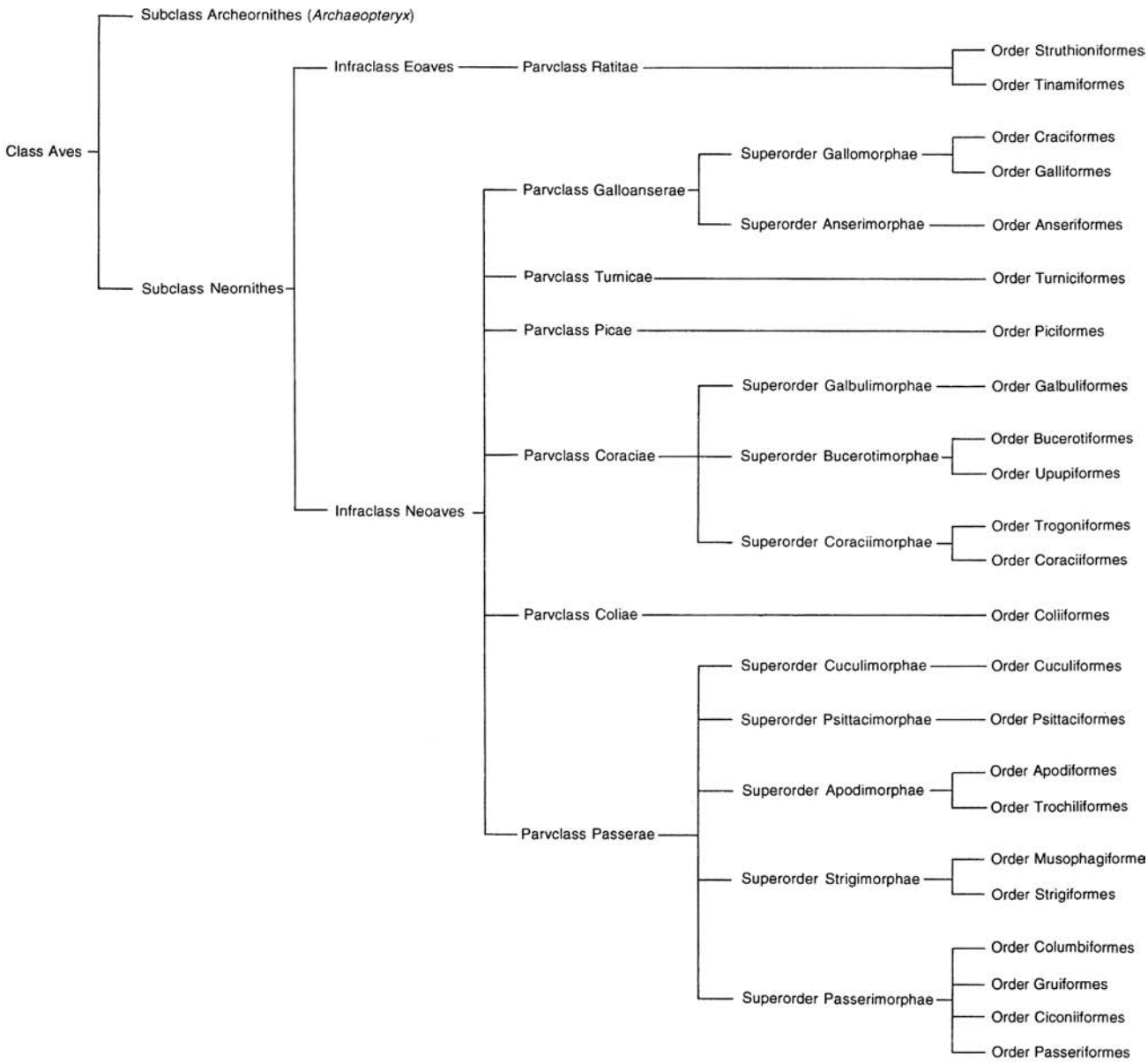


Figure 11.8. Biochemical classification of Aves (simplified from Sibley and Ahlquist 1990; Sibley and Monroe 1990).

regarding higher relationships among the major avian clades, the base of the avian tree appears to be well corroborated from both morphological and molecular data. Thus, modern birds can be divided into two basal clades: Palaeognathae (tinamous and ratite birds) and Neognathae (all other birds). Neognathae, in turn, are composed of two sister clades: Galloanserae (galliforms and anseriforms) and Neoaves (all remaining taxa of birds) (Mayr and Clarke 2003; Livezey and Zusi 2007; Dyke and Van Tuinen 2004). I have followed here the higher-order phylogeny of modern birds based on molecular systematics (Hackett et al. 2008).

Estimates for the timing of avian diversification have been based on molecular clocks or on the known fossil record. Molecular clocks suggest that the Palaeognathae-Neognathae split probably took place during the Early Cretaceous time (about 125 million years ago), while the Galloanserae-Neoaves split occurred around the Upper

Cretaceous (100 million years ago) and diversified soon after the KT extinction. Fossil evidence indicates substantially later dates for the temporal divergence of major superorders of modern birds. As more and more fossils are discovered, the discrepancy between molecular estimates and fossil evidence is narrowing down to a compromise.

Assembling the Avian Tree

Currently, the classification of modern birds (Aves) is in a state of flux; it is continually changing with new evidence from both molecular and morphological phylogenies to reveal their putative evolutionary history. Deep avian evolutionary relationships have been difficult to resolve as a result of their explosive evolution soon after the KT extinction. We have identified several adaptive radiations across the diversity of birds in space and time that may shed new light on the tempo and mode of evolution and their phylogenetic relationships. Cenozoic birds proliferated in both form and function, underwent a major adaptive radiation, and occupied different niches. The great variety of birds on different continents might be linked to plate movements during the Cenozoic, allowing different groups to evolve in isolation from one another, encouraging speciation and diversification. Modern birds occupy a wide diversity of niches and exhibit a variety of behaviors. We can broadly define several ecological types among radiation modern birds: flightless birds, groundbirds, several assemblages of waterbirds, birds of prey, shorebirds, seabirds, primitive landbirds, modern landbirds, and songbirds. However, adaptations to these environments clearly arose multiple times because many aquatic birds were not part of the "waterbird clade" and terrestrial birds were found outside the "landbird clade."

I have tried to preserve the ordinal names of Gadow with modifications and rearrangement of the composition of their members, when necessary, on the basis of recent morphological and molecular systematics. The names of clades above the ordinal ranks are printed in all capitals, the names of orders have the long suffix *-iformes*, family names end in *-idae*.

A detailed analysis of the evidence supporting avian relationships is beyond the scope of this book. Here I introduce the major taxonomic groups—called orders—of the birds of the world. The complete classification of modern, living birds is a hierarchical arrangement of 16 orders and 187 families, which include 2,030 genera and approximately 9,993 species. The numbers of orders, genera, and species will continue to change as revisions and discoveries are made. The systematic hierarchy of unranked major clades of Aves is as follows:

PHYLOGENETIC HIERARCHY
Subclass Avialae Gauthier, 1986
  Infraclass Carinatae Merrem, 1813
    Parvclass Aves Linnaeus, 1758
      Superorder Palaeognathae Pycraft, 1900
      Superorder Neognathae Pycraft, 1900
    Grandorder Galloanserae Sibley et al, 1988
    Grandorder Neoaves Sibley et al., 1988

AVES (Node A): (Modern Birds)

Phylogeny of Aves

Several clades of Aves, or modern birds, are now strongly supported by multiple lines of paleontological and molecular evidence, but the higher-order phylogeny is not fully resolved. Modern birds occupy a wide diversity of niches and exhibit a variety of behaviors. The broad structure of my phylogeny suggests diversification along general ecological divisions, such as waterbirds, shorebirds, landbirds, predatory birds, nocturnal birds, and perching birds. However, evolution to these adaptations clearly arose multiple times. In this discussion, I follow the cladogram of modern birds (fig. 11.10) to describe the major groups and their interrelationships, as we move in the cladogram from node A to node O. These fifteen nodes of birds are described below.

Traditionally, the Aves are divided basally into two sister taxa, or supergroups—Palaeognathae (ratites and tinamous) and Neognathae (all other modern birds)—on the basis of palatal configuration (Huxley 1867). Both cladistic analysis (Cracraft 1974) and molecular data (Sibley and Ahlquist 1990) support this basal dichotomy of Aves and monophyly of two sister taxa, Palaeognathae and Neog-

nathae. The different palatal structures of modern birds are linked to their different styles of feeding (fig. 11.6). It is widely believed that the avian palate can be derived from the basic archosaurian pattern with backward migration of the choanae, loss of the ectopterygoid, and development of palatal kinesis (Witmer and Martin 1987). The palaeognathous palate is the diagnostic feature of ratites and tinamous. In this type, the palatine and pterygoids are sutured in the primitive archosaur fashion; the vomer extends far back and articulates with the rostral ends of pterygoids; the elongate basipteryoid processes develop a flexible joint with the pterygoid.

The neognathous palate is characteristic of most flying birds. Here the basipterygoid processes are lost, a flexible joint is developed between the palatine and the pterygoid, and the vomers are reduced or lost. The movable pterygoid-palatine joint in the neognathous palate is an evolutionary novelty. Balouet (1982) considered virtually all other features of the neognathous palate to be consequences of pterygoid segmentation. The embryonic pterygoid in many neognaths splits into two portions: the rostral part becomes detached and fuses with the palatine, and the caudal part remains free and forms the adult pterygoid. Thus, a movable intrapterygoid joint is established between the rostral and caudal segments of an initially single bone but seems to lie between the pterygoid and the palatine in the adult. The adult palatine, in reality, is a compound bone, where the original palatine and the rostral portion of the pterygoid join to form a large element. The adult pterygoid is reduced and is represented by a stout bar connecting the parasphenoid rostrum with the condyle of the quadrate.

PALAEOGNATHAE (Node B)

Phylogeny of Palaeognathae

Extant Palaeognathae include volant Tinamidae and the flightless living groundbirds such as Rheidae (rheas), Struthionidae (ostriches), Casuariidae (emus, cassowaries), and Apterygidae (moas, kiwis). Although the monophyly of Palaeognathae is supported by palatal morphology and molecular evidence, their interrelations are highly controversial. The ratites and tinamous are an ancient group of birds that share a unique palatal configuration. The origin and evolution of palaeognathous birds have been debated incessantly. The question is whether they are a natural group or merely an assemblage of unrelated forms that have followed a parallel line of evolution. Monophyly of palaeognaths is now well corroborated, but relationships within the ratites remain difficult to resolve. Most authors united the flightless taxa as ratites and considered Tinamidae as the sister taxon on the basis of morphology (Cracraft 1974; Livezey and Zusi 2007). The living ratites have a flat sternum, reduced wings, and a lack of ossification between the ilium and ischium around the ilioischiadic fenestra. It is generally believed that ratites descended from flying ancestors that lost their powers of flight as they evolved into medium-sized, grazing animals. This idea is supported by the discovery of *Lithornis*, a volant palaeognath from the Paleocene and Eocene of Wyoming (Houde and Olson 1981). Because indisputable neognaths such as *Polarornis* were present in the Late Cretaceous, palaeognaths must have been present at the time as well. Most likely, lithornids extended in the Cretaceous, but so far definite members of this group have yet to be reported. Recent cladistic (Cracraft 1974) and biochemical (Sibley and Ahlquist 1990) analyses suggest that there are two basal lineages within the palaeognathous birds—tinamous and ratites. Cracraft (1974) recognized five successive clades in palaeognathous birds: Palaeognathae (Tinamidae + Ratiti), Ratiti (Apteryges + Struthiones), Struthiones (Aepyornithidae + Struthionoidea), Struthionoidea (Casuariidae + Struthionidae), and Struthionidae (Struthioninae + Rheinae) (fig. 11.9)

The ratites are a diverse clade of flightless birds that include ostriches, emus, rheas, cassowaries, and kiwis. They are united by a number of primitive characters, such as a palaeognathous palate, a keel-less sternum, an open ilioischiadic fenestra, weak and degenerated flight muscles, an atrophied wishbone, and retrogressed feathers. However, their legs are stronger for cursorial adaptation. They are mainly omnivores. Most likely, ratites originated in Gondwana continents from their flying ancestors.

Ratite classification is controversial, with some au-

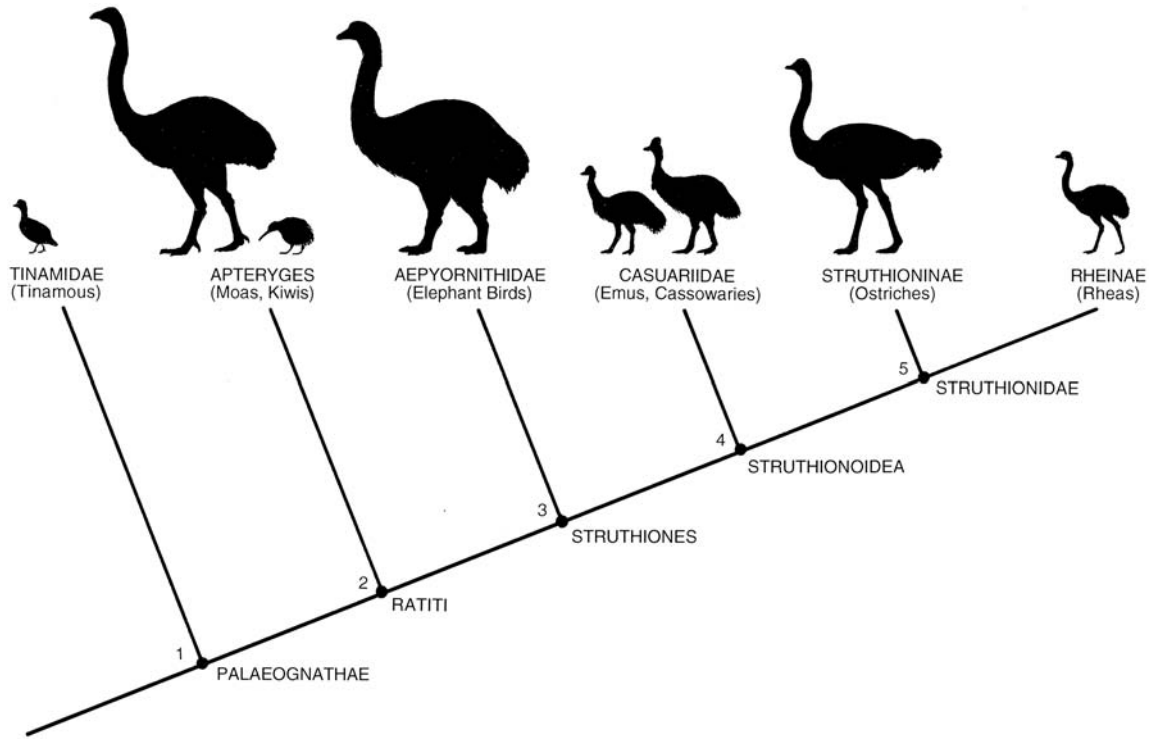


Figure 11.9. Phylogeny of palaeognathous birds (based on data in Cracraft 1974).

thorities placing all living groups in a single order, Struthioniformes (Sibley and Monroe 1990); others divide the ratites into Apterygiformes (three species of kiwi, all in New Zealand), Casuariformes (the emu of Australia and three cassowaries: one in northeastern Australia and two others in the New Guinea region), Struthioniformes (the ostrich of Africa), and Rheiformes (the greater and lesser rheas of South America) (Gill 1995).

Currently, there are fourteen genera and fifty-six species of living palaeognathous birds. We recognize six families of palaeognathous birds: Tinamidae (tinamous), Aepyornithidae (elephant birds), Dinorthidae (moas and kiwis), Casuariidae (cassowaries, emus), Struthionidae (ostriches), and Rheidae (rheas). Of these, only tinamous can fly; the other groups are flightless. There are ten living species of ratites, all restricted to southern continents: two species of rheas (*Rhea*) in South America, three species of cassowaries (*Casuaris*) in New Guinea, the emu (*Dromaius*) of Australia, three species of kiwis (*Apteryx*) in New Zealand, and the ostrich (*Struthio*) of Africa. With most species being flightless, a Gondwana origin of palaeognathous birds has been suggested in numerous studies (Cracraft 1974).

In contrast to morphology-based analysis, Hackett et al. (2008) concluded from molecular evidence that Palaeognathae is a monophyletic group, and that struthionids are the sister taxon of all other palaeognaths, such as rheids, tinamids, apterygids, and casuariids. They found that tinamous are not primitive within palaeognaths, but are among the most advanced. They placed the tinamous with ratites, more derived than ostriches or rheas, and as a sister group to emus and kiwis, and this makes ratites paraphyletic. Apart from features related to flightlessness, ratites show few unambiguous synapomorphies. This new molecular phylogeny means that the flightlessness seen in different ratite clades arose convergently at least four times. This would explain why ratites look so different in several features in the locomotory apparatus such as wing length and pelvis shape. Here I follow the molecular phylogeny of palaeognathous birds (fig 11.10).

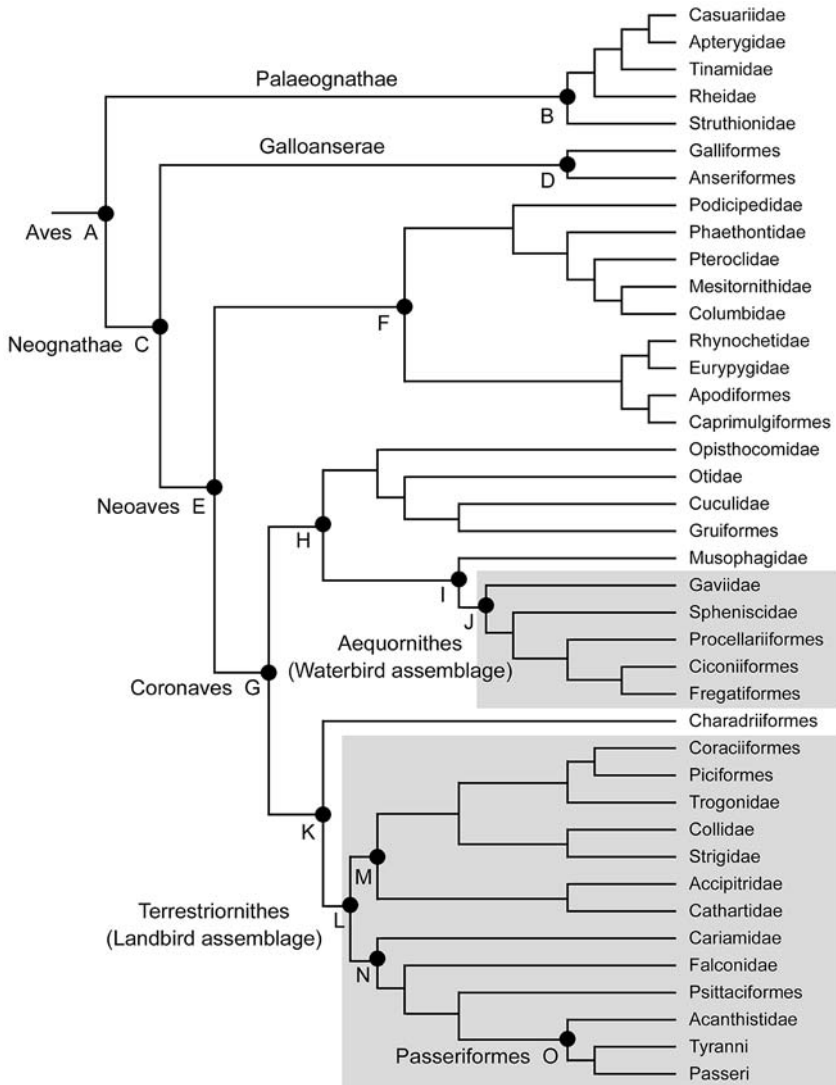


Figure 11.10. Phylogenetic relationships of Aves, or modern birds, based on molecular and morphological evidence. The Parvclass Aves comprises two superorders, Palaeognathae and Neognathae, and sixteen orders, whose members have been rearranged to achieve monophyly. The tentative cladogram shows ecological radiations of different clades from flightless birds to groundbirds to waterbirds to birds of prey to seabirds to primitive landbirds to modern landbirds that culminate in songbirds (modified from Hackett et al. 2008; Mayr 2010).

Palaeognathae contains five extant families: struthionids (ostriches), rheids (rheas), tinamids (tinamous), apterygids (kiwis), and casuariids (emus, cassowaries).

Struthionidae (Ostriches)

The most primitive palaeognaths are the struthionids. The ostriches may date back to the Eocene and were widely distributed during the Neogene period. Their fossils have been found in Europe, Africa, and Mongolia. Today only one species, *Struthio camelus*, remains. It is the largest living bird and inhabits the savanna or brushland of Africa. It can run faster than any other two-legged animal, and it lays the largest eggs of any living creature. The last ostriches in Arabia were killed during World War II. The ostriches have two toes (the third and fourth), and the lateral one seems to be in the process of vanishing. They

are large, flightless, cursorial birds with small wings and may grow to be 2.6 meters tall.

Stratigraphic range: Eocene-Holocene; living species: 1; length: 180 centimeters.

Rheidae (Rheas)

Rheas were restricted to South America throughout the Cenozoic. The two living species differ in size; the common rhea (approximately 1.4 meters) is taller than Darwin's rhea (approximately 90 centimeters). These flightless birds are capable of running long distances in the pampas. Rheas have small tails and only three toes; they lack an aftershaft in their loose, soft feathers.

Stratigraphic range: Lower Eocene–Holocene; living species: 2; length: 90–130 centimeters.

Tinamidae (Tinamous)

The tinamous are partridge-like birds that range from southern Mexico to the tip of South America. They have weak bills and small tails. Although tinamous have the keeled sternum essential for flight, they are clumsy fliers. They are actually most closely related to moas and kiwis and are considered to be an outgroup of the ratites.

Stratigraphic range: Upper Pliocene–Holocene; living species: 47; size: 15–50 centimeters.

Apterygidae (Kiwis)

The apterygids, or kiwis, include three species of small birds of New Zealand. They are mainly nocturnal, wingless, probing birds of forests, with their nostrils at the tip of their flexible bills. They mainly feed on insects, worms, and berries, as well as fallen fruits, seeds, and leaves. During the day, they sleep in hollow logs, in burrows, or under tree roots. Kiwis have been hunted for their meat and feathers and are now threatened with the introduction of predator mammals.

Casuariidae (Cassowaries, Emus)

Both cassowaries and emus are large, flightless, cursorial birds with diminutive wings. Cassowaries spend much of the day hidden in the dense jungles of New Guinea and adjacent islands. They have a bony crest, or casque, on the top of the head, like a helmet, which probably serves as a protective device and assists them in pushing through the dense tropical forest vegetation. The casque may help the birds turn over loose soil or sand when they search for food. Their diet consists mainly of fruit, seeds, and berries.

Emus, the world's second largest living birds, live in Australia and are the only extant member of the genus *Dromaius*. The soft-feathered brown birds stand more than 2 meters tall. They have long necks and long legs and live in open woodland, savanna, and agricultural habitats. They are omnivores, eating grasses and other vegetation, fruit, seeds, flowers, and insects.

Stratigraphic range: Pleistocene-Holocene; living species: 4; length: 130–190 centimeters.

Extinct Palaeognaths

Some of the most spectacular palaeognaths are now extinct: thirteen species of moas (Dinorthidae) of New Zealand, nine species of elephant birds (Aepyornithidae) of Madagascar, and eight species of mihirung birds (Dromornithidae) of Australia. These gigantic grazers were able to develop successfully because of their isolation from significant competitors or predators. It is likely that their ancestors flew to these islands and then became flightless. Their fossils and eggs have been recovered from Pleistocene and Holocene localities. Knowledge of the exact interrelationships of living palaeognaths may help placement of extinct taxa.

The fossil record of ratites is spotty; the oldest record, *Remiornis*, extends back to the Paleocene of France (Martin 1992). Another flightless form, *Palaeotis* from the Eocene Messel Oil Shale, is regarded as a close relative of the ostrich (Peters 1992, 1995). It shows weak development of the sternum, pectoral girdle, and wings. African ratites are known from Eocene and Oligocene deposits. The discovery of North American, European, and Mongolian ancestral ratites has zoogeographic implications; it argues against the popular notion that ratites evolved in Gondwana, a thesis based on their present distribution.

The aepyornithids, or elephant birds, are another extinct group of large flightless birds; they lived on the

island of Madagascar but were exterminated by human activity. They had long and powerful legs but retained vestiges of wings. The largest bird ever to exist, *Aepyornis maximus*, attained a height of more than 3 meters.

The extinct dinornithids, or moas, are generally grouped with kiwis. The moas are an extinct group of large, flightless, grazing birds that once flourished in New Zealand. Excessive hunting by Maori natives caused the extermination of these birds. There are twenty known species of moas; *Dinornis* stood more than 3 meters tall and probably weighed about 250 kilograms. The kiwis of New Zealand are the smallest and most anomalous of the ratites.

NEOGNATHAE (Node C)

Phylogeny of Neognathae

There are some nine thousand species of neognaths, by far the majority of living birds, but their interrelationships are highly controversial. Both morphological and molecular phylogeny classifies Neognathae into two sister taxa, or superorders: the Galloanserae (ducks, chickens, and their allies) and the Neoaves (all other neognaths), with reduction in the phallus being a neoavian character (see fig. 11.10) (Mayr and Clarke 2003; Livezey and Zusi 2007; Dyke and Van Tuinen 2004; Hackett et al. 2008). The relationships of orders and families within these two major clades are arranged in a sequence that attempts to follow the current views on neognath phylogeny, combining both morphological and molecular evidence (Hatchet et al. 2008).

The Galloanserae are generally considered the most primitive basal group of neognaths. All other neognaths are termed Neoaves. The basal radiation of Neoaves includes both waterbirds and landbirds (node F Metaves) such as podicipedids (grebes), phaethontids (tropic birds), pteroclids (sandgrouse), mesitornithids (mesites), and columbids (pigeons). The sister group of Metaves includes the largest clade of Neoaves, called Coronaves (node G), consisting of several groups of primitive terrestrial or arboreal birds, waterbirds (Aequornithes), landbirds (Terrestriornithes), as well as passeriforms (songbirds). Among neognaths, the passeriforms are the dominant and most derived birds represented by 5,700 species, containing more than half of the living species of birds. They show great variation in size and color and include all songbirds such as robins, finches, thrushes, sparrows, and jays, and have a complex syrinx system. Their feet are adapted to cling to branches automatically. Their fossil record is poor, especially from the Early Tertiary, but became numerous during the Miocene time. Some of the important clades of neognathous birds are described below.

GALLOANSERAE (Node D): (Galliforms and Anseriforms)

Both morphological and molecular data suggest that galliforms (fowl) and anseriforms (waterfowl) form the clade Galloanserae that represents the earliest divergence of the neognathous birds and includes galliforms and anseriforms. Huxley (1867) was among the first to comment on osteological similarities between galliforms and anseriforms on the basis of palatal morphology, the quadrate, and the lower jaw.

Galliformes (Chicken, Quail, Grouse, Pheasants, Turkeys)

Galliforms, or gamebirds, are all vegetarian, ground-feeding chicken-like birds with short, stout beaks, short rounded wings, and well-developed tails. Heavy feet are adapted to scratching the ground and running. They have strong breast muscles. Their wings are short and rounded; flight is explosive but not prolonged. They have precocial development; the young hatch fully covered with down, and they are able to run and feed. Many species use elaborate courtship displays and vocalizations for communication. Galliforms contain five families: phasianids (including chicken, quail, partridges, pheasants, turkeys, and grouse), odontophorids (New World quails), numidids (guineafowl of Ethiopia), cracids (guans, currasows, and chachalacas of Central and South America), and megapodes (mallee fowl and bush turkeys of Australia). They have strong, usually spurred legs that are well adapted for running and walking. They possess short rounded wings and elaborate tail feathers and can fly for short distances.

The oldest galliform birds are known from the Late Cretaceous sediments, based on isolated and fragmentary material; however, *Gallinuloides*, the Early Eocene fossil from the Green River Formation, is informative.

Stratigraphic range: Late Cretaceous–Holocene; living species: 250; length: 13–198 centimeters.

Anseriforms (Screamers, Waterfowl)

Anseriforms are gregarious waterbirds with webbed or long, unwebbed toes. They have broad bills containing many tactile nerve endings and filtering ridges, or "teeth," at the margins. They have short feet, which are often webbed. The clades include two families, Anhimidae (screamers) and Anatidae (such as ducks, geese, and swans); both have webbed feet and broad bills that contain fine plates or lamellae to aid in food handling and in straining food organisms from water. The screamers are large-footed marsh birds of South America, represented by three species. They are mainly marshland birds, but are also found in open savannas and on the banks of ponds. They can fly strongly and can soar to considerable heights. They have chicken-like bills, and they bear little resemblance to other waterfowl. They form morphological links between gamebirds and geese.

The anatids such as swans, geese, and ducks (collectively known as waterfowl) have a cosmopolitan distribution, occurring all over the world except Antarctica, and make many migrations over thousands of kilometers. There are thirty-seven genera of waterfowl. Although excellent fliers, these birds are adapted for swimming, floating on the water surface, and in some cases diving. Most waterfowl are associated with freshwater, at least during the breeding season. Members vary greatly in size; the largest, the mute swan, weighs more than 15 kilograms, and the smallest, the ringed teal, is about 300 grams.

Stratigraphic range: Late Cretaceous–Holocene; living species: 161; length: 29–160 centimeters.

The oldest fossil is *Polarornis* (= *Vegavis*) from the Late Cretaceous of Antarctica. Other genera such as *Presbyornis* from Lower Eocene deposits of North America and *Anatalavis* from the Lower Eocene London Clay are well represented.

NEOAVES (Node E)

Neoaves is a clade that contains 95% of all modern birds (Aves) with the exception of Palaeognathae and Galloanserae. Both molecular data and fossil evidence indicate a Late Cretaceous origin of Neoaves that underwent a strong increase in diversification in rapid succession of a stem group of modern neoavian taxa during the Paleocene-Eocene boundary, which filled the many vacant ecological niches after the KT extinction. As a result, the higher-level systematics of Neoaves and their timing and pattern of emergence remain largely unresolved. Here I follow the phylogeny of Hackett et al. (2008) to show the tentative relationships among the neoavian higher taxa. In their cladogram, major nodes of Neoaves remain unnamed because of the uncertainty of the relationships of the memberships of major groups. The tentative phylogeny of Neoaves with various unnamed nodes (E–O) is shown in figure 11.10.

Traditionally, there are twenty-three nonpasserine orders within Neoaves. Of these, nine consist of just a single family: Sphenesciformes (penguins), Gaviiformes (loons), Podicipediformes (grebes), Phoenicopteriformes (flamingos), Opisthocomiformes (hoatzin), Pterocliformes (sandgrouse), Columbiformes (pigeons), Colliformes (collies), and Trogoniformes (trogons). These orders are treated here as families.

The basal radiation of Neoaves is designated here as node E. Some analyses (Hackett et al. 2008) have divided Neoaves into two distinct clades: a primitive Metaves (node F) and a more derived Coronaves (node G). Metaves comprises the basal radiation of Neoaves, including podicipedids (grebes), phaethontids (tropicbirds), pteroclids (sandgrouse), mesitornithids (mesites), columbids (pigeons), rhynochetids (kagu), eurypygids (sunbittern), apodiforms (hummingbirds), and caprimugiforms (nightjars), while Coronaves includes the remaining neoavians.

Waterbirds are generally considered the basal radiation of Neoaves. Many authors have suggested in the past that some or all of the waterbird orders, such as marine procellariiforms (albatrosses, shearwater, fulmar), sphenesciforms (penguins), gaviiforms (loons), ciconiiforms (storks,

herons, flamingos), pelecaniforms (pelicans, cormorants), charadriiforms (shorebirds and gulls), and gruiforms (cranes, rails) are closely related to one another (Sibley and Ahlquist 1990; Feduccia 1996). However, recent phylogenetic study suggests that waterbirds may not be related to one another as a whole but are somewhat punctuated by landbirds across the phylogeny (Hackett et al. 2008). Recent phylogeny of modern birds (fig. 11.10) revealed two highly supported ecologic clades: a waterbird assemblage and a landbird assemblage. Mayr (2010) named the waterbird clade as Aequornithes (node J), whereas I designate here the landbird clade as Terrestriornithes (node L).

METAVES (Node F)

Metaves, the basal radiation of Neoaves, includes the following clades: Podicipedidae, Phaethontidae, Pteroclidae, Mesitornithidae, Columbidae, Rhynochetidae, Eurypygidae, Apodiformes, and Caprimugiformes.

Podicipedidae (Grebes)

The podicipedids, or grebes, are highly specialized, foot-propelled, freshwater diving birds with lobed toes and soft and silky plumage. These graceful aquatic birds are often mistaken for ducks when seen swimming on freshwater lakes and ponds. Some species visit the sea when migrating and in winter. The legs are short and located so far back on the body that locomotion on land is awkward. They have many loon-like characteristics, such as long necks, pointed beaks, highly enlarged cnemial crests, and minute tails. Bills vary in size and shape (from short to long and pointed forms) that indicate their different food preferences ranging from fish to freshwater insects and crustaceans. The grebes are distributed globally, with most in the New World. They have narrow wings and are weak fliers; indeed, two species are secondarily flightless. Unlike in loons, the patella and the tibia form the cnemial crest of tibiotarsus in grebes. The toes are lobed and the tarsi are laterally compressed, thereby offering little resistance when drawn forward through the water during propulsion. Grebes form monogamous pairs and both sexes take part in ritual courtship ceremonies.

Stratigraphic range: Lower Miocene–Holocene; living species: 22; length: 21–66 centimeters.

Phaethontidae (Tropicbirds)

The phaethontids, or tropicbirds, are medium-sized seabirds, which were traditionally allied to pelicaniforms. Three species of tropicbirds belong to a single genus *Phaethon* and they range in size from 76 centimeters to 102 centimeters. They have worldwide distribution along the tropical regions. They have white plumage and elongated central tail feathers and are excellent fliers but awkward when walking. Tropicbirds are adapted for obtaining their prey by plunge diving in tropical and subtropical seas. The bill is stout, pointed, and slightly decurved with serrated edges. They eat mainly flying fish, squid, and crustaceans from the surface of the water. They fly long distances in search of prey. They nest in cavities in cliffs, in rainforest trees, and under bushes. The oldest fossils are known from the Eocene period.

Pteroclidae (Sandgrouse)

The pteroclids, or sandgrouse, are pigeon-sized birds that range in size from 24 to 40 centimeters. They are mainly ground-dwellers, moving with a shuffling gait, and feed on small seeds. They are patterned cryptically in shades of brown, yellow, olive, gray, and white for camouflage in the dusty landscape of arid and semiarid regions. There are about sixteen species of sandgrouse restricted mainly to Africa and Eurasia. With their long and pointed wings, sandgrouse are powerful fliers. They fly long distances to make daily visits to waterholes where they gather in large numbers, sometimes in the thousands, to drink.

Mesitornithidae (Mesites)

The mesitornithids (mesites) are a family of small, nearly flightless groundbirds endemic to Madagascar that feed on insects and seeds. They use their long bills to probe in the soil and make sharp calls for territorial defense. Currently, there are three species that are on the verge of extinction. The systematic position of this group of bird is uncertain, but they are generally allied to doves.

Columbidae (Pigeons and Doves)

The columbids such as pigeons and doves are small to medium-size birds ranging in size from 15 to 84 centimeters. They have small heads, short bills, compact bodies, and short necks and legs. The wings and tail show much variation; some of them are brightly colored, others rather drab. The columbids comprise 310 species that are found in most parts of the world, often in large numbers, in a wide range of habitats from arid grasslands to tropical rainforests to mountain slopes. Some species are terrestrial, but most perch in trees; others dwell in cliffs, and some roost on buildings in towns and cities. Pigeons are somewhat larger than the doves, but are closely related. They are fast-flying birds with long, pointed wings, a well-developed sternum, thick plumage, and a weak bill. These are tree- or ground-inhabiting birds that feed mainly on seeds and fruits. They feed their young with "crop milk" secreted from the lining of the crop of the adult birds—a trait unique to the family. Flightless forms, such as dodos and the solitaires of the Mascarene Islands, became extinct during the eighteenth century.

Stratigraphic range: Eocene-Holocene; living species: 307; length: 15–84 centimeters.

Rhynochetidae (Kagu)

The rhynochetids, or kagu, are crested, long-legged, flightless groundbirds endemic to the forests of New Caledonia, but their systematic position has been debated. It is a highly endangered bird with the introduction of predators. Most of the time it feeds on small invertebrates from the ground with its pointed bill. Recent molecular phylogeny suggests that it might be a sister taxon to caprimugiforms.

Eurypygidae (Sunbittern)

The family eurypygids, or sunbittern birds, contains a sole species. These birds are found in humid tropical regions of the Americas, ranging from Mexico to Peru. They are small, cryptic birds, about 46 centimeters in length, with a long stout body, a long slender neck, and a relatively small head. They display their large wings when threatened.

Apodiformes (Hummingbirds, Swifts)

Apodiforms are fast, acrobatic birds that that feed on the wing, eating insects and nectars. Flying from flower to flower, the hummingbird pollinates the plants on which it feeds. Its long beak is ideal for feeding on nectar. Hummingbirds (Trochilidae) and swifts (Apodidae) have powerful flight muscles and short feet with sharp claws that enable them to cling on perches.

Stratigraphic range: Upper Eocene–Holocene; living species: 422; length: 6.3–23 centimeters.

Caprimugiformes (Nightjars, Frogmouths)

Caprimugiforms are mainly cryptically colored nocturnal birds, with long, pointed wings, weak feet, small bills, and large mouths for catching insects. They are known from all continents except Antarctica. They include several poorly known groups such as nightjars, frogmouths, potoos, and oilbirds. They resemble owls in their shape and nocturnal hunting habits.

The aegothelids, or owlet-nightjars, are small nocturnal birds. They comprise nine species, which are restricted to the forests of New Guinea, Australia, Moluccas, and New Caledonia. They look like a cross between owls and nightjars because of their upright stance. They are small to medium-size, ranging from 18 to 30 centimeters. They are insectivores, usually hunting flying insects in the air but sometimes on the ground.

CORONAVES (Node G)

Coronaves, the derived clade of Neoaves, includes the following groups: Opisthocomidae, Otididae, Cuculiformes, Gruiformes, and Musophagidae + Aequornithes (node J) + Terrestriornithes (node L). The basal radiation of Coronaves is represented by several clades of primitive terrestrial or arboreal birds such as opisthocomids (hoatzin), otidids (bustards), cuculiforms (cuckoos), gruiforms (rails and cranes), and musophagids (turacos).

UNNAMED (Node H)

This node contains several archaic landbirds such as Opisthocomidae, Otidae, Cuculidae, Gruiformes, Musophagidae, as well as waterbird assemblage Aequornithes (Node J).

Opisthocomidae

The only living representative of the family is the Hoatzin, *Opisthocomus hoazin*, an intriguing tropical bird found in swamps, riverine forest, mangroves of the Amazon, and the Orinoco delta in South America. Approximately the size of a turkey, it is about 65 centimeters long, with brown plumage, a long neck, a long tail, and a small bluish head that sports a spiky rufous crest. Hoatzins are poor fliers because the wing feathers are loosely attached. They nest on a tree branch over water. When alarmed, nestlings jump into the water from the overhanging branches and then climb to another tree. The hoatzins subsist on a diet of leaves, flowers, and fruits of marsh plants. Hoatzin chicks have wing claws like those of maniraptorans and avialans, by which they climb, crawl, and clamber through the tree branches. They have elongated forelimbs, semilunate wrist joints, elongated penultimate phalanxes, and terminal claws as in maniraptoran dinosaurs and provide an evolutionary glimpse at the wing-assisted climbing adaptations of feathered coelurosaurs.

Otididae (Bustards)

The otidids, or bustards, form a phylogenetic barrier between two waterbird assemblages, gruiforms and pelicaniforms. The bustards are large and highly terrestrial birds that are adapted to dry open country and steppes in the Old World. The family is completely restricted to the Old World. Of the ten genera, a few are Eurasian, one is Australian, and the remainder are purely African. They include some of the heaviest flying birds such as the kori bustard and great bustard exceeding a mass of 20 kilograms. These birds take off only with great difficulty by running like taxiing aircraft. The legs are fairly long and strong; the tibia is featherless. Bustards are omnivorous and opportunistic, feeding on seeds and large insects such as grasshoppers and locusts.

Cuculidae (Cuckoos, Coucals, Roadrunners)

The cuculids are a diverse family of medium-size slender birds that range in size from 16 to 70 centimeters. There are about 142 species with cosmopolitan distribution, except Antarctica. Most of the species are arboreal, but some species remain terrestrial. The legs are short in majority of arboreal species, but long in those that live on the ground. The wings vary from moderately long and rounded to long and narrow. Some members of the family are known as anis, couas, coucals, malkohas, and roadrunners. They have a greatest diversity in the Old World tropics, occupying a great range of habitats including tropical rainforest to wetland to desert. They are omnivores, though most species rely on caterpillars. Many large terrestrial cuckoos eat lizards and snakes. The cuckoos have distinctive zygodactyl feet for perching, where the two inner toes point forward and the two outer toes backward. They have long decurved bills and tails. Many Old World female cuckoos often deposit their eggs in the nests of other birds, leaving the hosts to raise their young (brood parasitism).

Gruiformes (Rails, Trumpeters, Cranes)

The gruiforms currently include three living families—Rallidae (rails), Psophiidae (trumpeters), and Gruidae (cranes)—and several extinct forms. Most gruiforms inhabit a marsh environment and are ground-nesting wading birds, but a few live on dry land and some even in deserts. Most species rarely fly, but some have managed to colonize oceanic islands. The Gruiformes are an ancient order that includes large flightless forms such as phorusrhacoids and diatrymas. *Messelornis* from the Upper Paleocene of France, Lower Eocene of North America, and Middle Eocene of Germany provide a glimpse of the early radiation of this clade.

Stratigraphic range: Paleocene-Holocene; living species: 185; length: 11–152 centimeters.

The rallids (rails) are small to medium-sized marsh birds, although some species are terrestrial. They super-

ficially resemble fowls and range in size from a sparrow to heavy flightless forms the size of a goose. They have short rounded wings, large legs and feet, flattened bodies, and small, often degenerate tails. They are weak fliers, and often prefer to run rather than fly, but members of some populations migrate long distances to colonize islands. As a result, many island species become secondarily flightless forms. There are about 143 species worldwide, but they are absent in deserts and polar regions. They are highly territorial and opportunistic omnivores, feeding on a wide variety of plants and animals.

The psophiids, or trumpeters, are secretive, gregarious, ground-dwelling birds of the rainforests of South America; they are about the size of a domestic chicken. They have long necks; a short, stout, and slightly curved bill; moderately long legs; very rounded wings; and a short tail. They roam about the forest floor and eat berries, fruits, and other vegetables. They roost in trees, and fly infrequently and with considerable effort. They are highly vocal and are named for their voice. They comprise only three species, which are predominantly glossy black in color.

The gruids, or cranes, are large, elegant wading birds with long necks and legs, with large wingspans ranging from 1.8 to 2.2 meters. These graceful birds have been admired for millennia and immortalized in artwork and literature. They are the tallest flying bird, ranging in height from 0.6 to 1.5 meters. Most cranes have white, gray, brown, or blue plumage with black primaries. There are fifteen species of cranes worldwide and most species are migratory. They fly with necks fully extended like pterosaurs, often in flocks, and sometimes soar to great heights. They live on all continents except Antarctica and South America. Many species of cranes are threatened owing to their large size, habitat loss, and active hunting. Primarily wetland and open-country birds, cranes forage by walking slowly and steadily in water or on swampy ground, searching for food. They are opportunistic feeders and eat a wide variety of plant material and small animals, picked off ground or dug up with their bills. Both sexes of cranes have spectacular and noisy courtship dances prior to the breeding season that have inspired artists and choreographers; they are territorial and monogamous. Crane fossils have been found from the Eocene period.

MUSOPHAGIDAE (Node I)

Musophagidae (Turacos and Allies)

The musophagids, or turacos, are large, colorful, long-tailed arboreal birds of sub-Saharan African forests, which include "banana-eaters" and "go-away" birds. They are large birds, about 37 to 76 centimeters long with conspicuous crests, short and strong bills, and broad and long tails. They are known for their brilliant plumage, usually glossy blue, green, or purple, with a prominent crest and have long been hunted for their feathers, which are used in the ceremonial headdresses of various African groups. They have short, rounded wings, and their flight is weak, but they run quickly through the tree canopy. They feed mostly on fruits as well as flowers, leaves, and buds with their strong, serrated bills. Recent molecular phylogeny indicates that musophagids may be a sister taxon of a large group of oceanic birds such as loons, penguins, procellariiforms, and pelicaniforms. The family contains twenty-three species, all confined to Africa. Turacos are weak fliers, and fly from tree to tree using phugoid gliding. However, they are highly acrobatic at moving, running, and hopping along branches. They eat a wide range of food, including fruits, leaves, buds, flowers, caterpillars, moths, and beetles. The fossil genus *Vefliontis* from the Miocene of France has been referred to musophagids.

AQUEORNITHES (Node J)

Aqueornithes represents the radiation of several groups of waterbird assemblages, including the Gaviidae, Sphenisciidae, Procellariformes, Ciconiiformes, and Fregatidae. Over the years, many authors have suggested that some or all of the waterbird orders, particularly the seabirds, are closely related to one another (Olson and Feduccia 1980; Cracraft 1998; Sibley and Ahlquist 1990). Recent molecular phylogeny (Hackett et al. 2008) contradicts the traditional view that all waterbirds are related to one another within Aves. However, some seabirds such as gaviiforms (loons), sphenesciforms (penguins), procellariiforms (tube-nosed birds), ciconiiforms (storks and allies),

and fregatiforms (frigates birds and allies) cluster to a clade Aequornithes (fig. 15.10, node J). Within this waterbird cluster, the large traditional orders of waterbirds such as ciconiforms and pelecaniforms are not monophyletic and selected taxa define the core group of these two orders. Since the family Pelecanidae has been allocated to ciconiiforms (Hackett et al. 2008), the residual taxa of older pelecaniforms such as Fregatidae (frigatebirds), Phalacrocoracidae (cormorants), and Sulidae (gannets) are accommodated into a new order, Fregatiformes, to avoid nomenclatural confusion. Moreover, the charadriiforms appear to be more specialized from this seabird clusters and are placed in a close group of landbirds (Terrestriornithes, node K). The second radiation of waterbirds has adapted to life within the marine environment. The terrestrial musophagids (turacos) form the close sister taxon of the second assemblages of water birds.

Gaviidae (Loons)

The gaviids, or loons, are small, heavy, foot-propelled diving birds with spear-shaped bills, stocky necks, streamlined bodies, and three webbed toes. They are a Holarctic family, found in many parts of high latitudes of North America and northern Eurasia. All five living species of loons are members of the genus *Gavia*. Superficially they resemble certain grebes, but they differ externally from the grebes by a combination of a dagger-like bill, a short neck, rough plumage, and lack of paddle-like lobes on the toes. The loons are large, bulky waterbirds that migrate during breeding season. Their wingspans range from 90 to 124 centimeters. The legs are short and located far back on the heavy body. The cnemial crest is formed entirely by the tibia. They mainly forage on fish with their streamlined, dagger-like bills in underwater pursuit, and they have flattened tarsi to reduce drag. They have denser bones than most birds to help them dive, and denser plumage to keep them waterproof and warm. The loud, haunting calls of loons are familiar sounds in the northern wilderness that create the sense of being apart from civilization and closer to the prehistoric time.

Stratigraphic range: Eocene-Holocene; living species: 4; length: 66–95 centimeters.

Spheniscidae (Penguins)

The sphenescids such as penguins are specialized diving birds of the Southern Hemisphere that have completely lost the power of flight. They can dive down 800 meters in search of food. They retain a deep keel and flipper-like wings for underwater propulsion. The wings lack flight feathers and cannot be folded because the bones of the wings are flattened and fused. Instead, they developed very efficient flippers for locomotion underwater. The legs are set well back along the body and bear webbed feet and strong nails that allow an erect posture. The feet are used for steering and braking underwater and for clambering up rocky shorelines. Represented by some six genera and seventeen living species, penguins pursue fish, squid, and crustaceans under the sea. The largest species, Emperor, stands 1 meter tall. Dense, short feathers and a heavy layer of fat insulate penguins from the extremely cold waters they inhabit. Penguins have a rich fossil record from Antarctica.

Stratigraphic range: Eocene-Holocene; living species: 17; length 40–120 centimeters.

Procellariiformes (Albatrosses, Shearwaters, Petrels)

Procellariiforms are large oceanic birds such as albatrosses, shearwaters, and petrels, with webbed feet, prolonged tubular nostrils, long narrow wings, and a characteristic musky smell. The nasal tubes entering into the bill may serve as outlets for excess salts taken into the system. The rhamphotheca of the bill is divided into plates. Procellariiformes includes several marine birds such as albatrosses, shearwaters, fulmars, and storm petrels. Many species have long, high-aspect ratio wings, held stiffly and used for soaring over the waves. Members of this group spend most of the time soaring above the oceans and only come to land for nesting. They are most diverse in the oceans of the Southern Hemisphere.

Albatrosses (Diomedeidae) are among the largest flying birds with long wings and long, heavy bills that feed on fish, squid, and krill. The largest is the wandering albatross, about 1.1 meter long with a wingspan to 3.5 meters. Albatrosses are superb soaring birds that use dy-

namic soaring of differential wind shear across the ocean to cover great distances. Of the twenty-one species of albatrosses, nineteen are threatened with extinction because of human activity.

Shearwaters are medium-sized, long-winged seabirds containing thirty species, which are common in temperate and cold waters. Petrels comprise forty-two species of mid- to large-size seabirds with wings and hooked bills that are very similar to shearwaters. Both shearwaters and petrels are excellent fliers; some use dynamic soaring like albatrosses, while others use alternate flapping flight with gliding. They feed at sea on squid, fish, and crustaceans.

Stratigraphic range: Middle Eocene–Holocene; living species: 81; length: 14–135 centimeters.

Ciconiiformes (Storks, Ibises, Spoonbills, Flamingos, Pelicans)

The ciconiiforms are long-necked and long-legged waders that followed the radiation of procellariiforms. The systematic relationships of the taxa placed in this order are highly controversial. Ciconiiforms are large, fish-eating, long-legged wading birds with long bills, long necks, and broad wings. Currently, pelicans are included within Ciconiiformes. The order Ciconiiformes has undergone many changes in its composition and includes several families: ciconiids (storks), pelecanids (pelicans), balaenicipitids (shoebill stork), ardeids (herons, egrets, bitterns), threskiornithids (ibises and spoonbills), and phoenicopterids (flamingos).

Stratigraphic range: Oligocene-Holocene; living species: 119; length: 28–152 centimeters.

Ciconiids, or storks, are large, long-legged, long-necked wading birds with long, stout, decurved bills. They forage on frogs, fish, insects, earthworms, small birds, and small mammals in shallow waters. There are nineteen living species of storks that occur on all continents except Antarctica in tropical and temperate regions; many species are migratory. They lack a syrinx and are mute. The storks are excellent soaring birds with wingspan averaging 1.5 meters. The marabou stork of Africa, the largest, stands up to 1.5 meters tall and has a wingspan of 3.2 meters; it is similar in size to the condor, placing it among the largest flying birds.

Pelicans are large water birds ranging in body mass from 5 to 11 kilograms with the larger species having wingspans up to 2.7 meters. They are highly adapted for swimming and flying, but are ungainly on land. They have a long beak and large throat pouch suspended beneath the lower jaw as a scoop net for trapping fish and squeezing out water before swallowing. The family is restricted to the temperate and tropical regions of both the Old and New Worlds, as well as Australia. Pelicans frequent inland and coastal waters, where they forage on fish and crustaceans. The earliest record of pelicans comes from the Lower Miocene of France; a beak has been recovered from the Oligocene strata of France.

Balaencipitids, or shoebills, are large stork-like birds with massive shoe-shaped bills. They are distributed in dense freshwater swamps and marshes of Central Africa. They are tall and large birds ranging in body mass from 4 to 7 kilograms, and are excellent soarers. Some fossil forms such as *Goliathia* and *Paludavis* are known from the Neogene deposits of Africa.

The ardeids, or herons, are medium to large wading birds with long bills, long necks, and long legs. They are freshwater and coastal birds with a cosmopolitan distribution. They have a long and harpoon-like bill for foraging aquatic animals.

Stratigraphic range: Eocene-Holocene, living species: 13; length: 91 centimeters.

Threskiornithids, such as ibises and spoonbills, have global distribution and include thirty-four species of large wading birds. They vary in size from 48 to 107 centimeters. Ibises have long, slender, decurved, curlew-like bills that are adapted for obtaining food by probing shallow water, mud, and grass for small animals; spoonbills have long, straight, spoon-shaped bills that are used for catching floating prey in shallow water. They are excellent soaring birds. In sustained flight, the head and neck are stretched forward and slow, flapping wingbeats alternate with short glides.

Phoenicopterids, or flamingos, are large, brilliantly colored wading birds, which live in alkaline and saline

lakes and lagoons. Once widespread, the five living species of flamingos have a broad but highly specialized distribution, occurring in parts of Mexico, the Caribbean, South America, and the Old World. They are large birds, about 1 to 2 meters in length, with long sinuous necks, long legs, down-curved bills, and webbed feet. They are filter feeders; the bill is sharply bent in the middle; the lower mandible is large and trough-like, the upper one is small and lid-like, lined with a series of lamellae. The bill is held upside down in the water and minute organisms are filtered by the fine lamellae. In feeding the mouth is opened and water enters along the entire length of the gape; when the gape is closed, the tongue forces water back through the filtering device.

Fregatiformes (Frigate Birds, Gannets, Cormorants, Anhingas)

The ciconiiforms are the sister group to the newly defined order of seabirds, the Frigatiformes (accommodating residual taxa of Pelecaniformes) that includes Fregatidae (frigate birds), Sulidae (gannets), phalocrocoracids (cormorants), and Anhingidae (snake birds). Fregatiforms are large, fish-eating waterbirds with all four toes webbed for swimming. They are strong fliers but poor walkers. All have some form of flexible throat pouch that allows them to hold large fish. They have long beaks that may be hooked, pointed, or straight. Their salt glands are located within the orbit. Among the living families, the frigate birds show the earliest record.

The fregatids, or frigatebirds, are large seabirds with iridescent black feathers. Their long, narrow, and high-aspect ratio wings and tail and extremely light skeleton make them excellent soaring birds. There are five species in the single genus *Fregata* with worldwide distribution over tropical oceans. The frigatebirds are designed for aerial life, having the lowest wing loading of any bird with a wingspan of 1.7 to 2.4 meters and an inability to land on water. They exploit thermals along the equatorial belt and soar day and night in a succession of climbs and descents in the direction of travel. These birds do not swim, cannot walk well, and cannot take off from the ground. They are adapted for drinking and feeding on the wing from the water surfaces and for nesting and roosting on the branches of trees and bushes. They are notorious for pirating food from other seabirds. The males have a red gular pouch that is inflated during mating season to attract females. The earliest frigate birds date from the Eocene period.

The sulids (boobies and gannets) are large, coastal seabirds of tropical and subtropical waters, known for their densely packed breeding colonies on islands and in cliffs. There are nine living species of the family, some of which are vulnerable. The sulids are about 60 to 85 centimeters long with a wingspan of about 140 to 175 centimeters and have a long tail; the wings are long, narrow, and pointed. They are excellent fliers with their streamlined bodies and high-aspect ratio wings and plunge-drive for fish and squids. They have stout legs and webbed feet, with the web connecting all four toes.

The phalacrocoracids, or the cormorants, the successful fishing birds, are represented by some forty species. They are sister groups of frigatebirds in this new phylogeny. Cormorants are medium to large seabirds with long necks and long bills with a hooked tip. Their feet have webbing between all four toes. The Northern Hemisphere species have black plumages; some Southern Hemisphere species are black and white. They range in size from 45 to 100 centimeters. They inhabit coasts and inland waterways over much of the world and feed on small eels, fish, and even water snakes.

The anhingids (anhingas), or snakebirds, are tropical and subtropical freshwater birds with a long S-shaped neck and a long pointed bill. They are large birds with an average body length of 85 centimeters and a wingspan of 120 centimeters with dark plumage. They are found in freshwater ponds and swamps where there is thick vegetation and tall trees. With their log and sharp bills, anhingas spear fish, flip them in the air, and swallow them headfirst. During swimming, the body remains submerged but the head and neck is stretched flat out on the surface of the water, making the bird look like a snake ready to strike. They do not have external nares and breathe through the epiglottis. There are four living species, and the family has a global distribution.

UNNAMED (Node K)

Recent molecular phylogenetic analysis suggests that charadriiforms are the sister group of a series of landbirds such as cathartids, accipitrids, strigiforms, coliiforms, trogoniforms, and coraciiforms.

Charadriiformes (Auks, Gulls, Terns, Sandpipers, and Plovers)

The Charadriiformes is a diverse order of water-feeding shorebirds that include several families such as alcids (auks), larids (gulls, terns), scolopacids (sandpipers), and charadriids (plovers and lapwings), but their interrelationships are controversial. Some, such as plovers and sandpipers, are the familiar shorebirds with long legs, which usually feed on small animals in mud or water. The Lari include gulls and terns, which have webbed feet and are noted for their long migrations. They feed by plunging into the water for fish, robbing other birds, or scavenging. The third group, the Alcae, is made up of wing-propelled divers, rather like penguins, which feed on fish or invertebrates.

The charadriiforms are small to medium-size, ranging from 12 to 66 centimeters. They have long legs and slim bills, and they seek tiny invertebrates and other small animals by wading in shallow water. The charadriiforms include about 350 species and are distributed worldwide. They often breed in large colonies and undergo long-distance migrations. *Graculavis* from the Late Cretaceous of New Jersey is often considered the oldest charadriiform fossil.

The alcids, or auks, are a successful group of wing-propelled divers that are similar to penguins ecologically, their counterparts in the southern oceans. The twenty-three species in the family vary in length from 16 to 76 centimeters with a large head, a short neck, a compact body, short wings, and a short tail. There is a considerable variation in bill structure in this group. They have black-and-white plumage and an upright posture like penguins, and they share similar habits because of convergent evolution. They are poor fliers but excellent divers and underwater swimmers in pursuit of fish, using their wings for propulsion. The webbed feet are placed well back on the body, which aids in swimming. They are restricted to the cold waters of the Southern Hemisphere. They come ashore during breeding season, usually in colonies on isolated islands and coastal cliffs.

Gulls and terns are the most common group of medium to large aerial birds along the coastal regions in temperate regions that feed, roost, and breed in densely packed colonies. They have moderately long legs with three fully webbed toes that allow them to swim effortlessly on the surface of water. They have long and narrow wings and soar gracefully in updrafts. Most gulls feed on fish and marine invertebrates, but they are opportunistic omnivores. Many species of gulls have learned to coexist with humans very successfully and scavenge their food from landfills. They are predominantly white-bodied as adults and range in length from 25 to 75 centimeters. Terns eat mainly fish. Most terns are also white but they have more slender bodies and are smaller than gulls. The Arctic terns are one of the long-distance migrants during their breeding season as they move southward to Antarctica; the round-trip journey is about 50,000 kilometers per year.

The scolopacids, or sandpipers, are a large family of waders, associated with coastlines, inland wetlands, and grasslands that comprise eighty-five species that are distributed worldwide. The greatest diversity of breeding species inhabits the higher northern latitude and many species undertake long annual migrations. Sandpipers have long bodies and legs and narrow wings. Depending on feeding habits, bills are short or curved and vary in length from short to long. They are small to medium-sized birds, measuring from 12 to 66 centimeters in length, the largest being the curlews, which have extremely long down-curved bills. The bills are sensitive and are used to probe for food. Many species of sandpipers are vulnerable because of habitat loss.

The charadriids, the plovers and lapwings, are small to medium-sized birds. The plovers have compact bodies, short necks, and long pointed wings. The lapwings are larger than the plovers and have rounded wings. They range in size from 12 to 38 centimeters in length. The

family contains about sixty-seven species that are distributed in open habitats essentially worldwide, being common on beaches and around many kinds of wetlands. Their bills are usually straight and they feed day and night on insects, spiders, small worms, and seeds. Most charadriids are brownish above and light below. They are territorial during breeding season. Because of habitat destruction and the introduction of mammal predators, some species are currently endangered.

TERRESTRIORNITHES (Node L)

Terrestriornithes, the radiation of the landbird assemblage, includes the cathartids (New World vultures), accipitrids (hawks, eagles, Old World vultures), strigids (owls), collids (cuckoos), trogonids (trogons), piciforms (woodpeckers), coraciiforms (rollers, kingfishers), and passerines (songbirds). Traditionally, the New World vultures were included in the ciconiforms along with storks and flamingos. Recent morphological and molecular data suggest that New World vultures (cathartids) and Old World vultures (accipitrids) are sister taxa (fig. 15.10, node E). The monophyly of traditional coraciiforms is not supported by recent molecular phylogeny, but several families of arboreal taxa within coraciiforms such as picids (woodpeckers), indicatorids (honey-guides), capitonids (barbets) buconids (puffbirds), and gallubulids (jacamaras) form a clade Piciformes. The rest of the taxa are kept within Coraciiformes.

UNNAMED (Node M)

Within Terrestriornithes, there are two unnamed nodes, Node M (coraciiforms + Piciformes + Trogonidae + Collidae + Strigidae + Accipteridae + Cathartidae) and Node N (Cariamidae + Falconidae + Psittaciformes + Node O).

Coraciiformes (Rollers, Kingfishers, Hornbills)

Coraciiforms are colorful birds largely of the Old World, including rollers, kingfishers, bee-eaters, and hornbills with large plumed heads, strong pointed bills, rounded wings, and small syndactyl feet, with the third and fourth toes joined at the base. They feed on a wide variety of prey, including worms, arthropods (insects, spiders, and scorpions), fish, aquatic invertebrates (crabs and shellfish), and small vertebrates. Most coraciiforms nest in the hollows of trees.

Stratigraphic range: Oligocene-Holocene; living species 387; length: 9–61 centimeters.

Coraciids such as rollers are highly colorful, acrobatic near-passerine birds that hunt insects and other small prey. The bill is moderately long, downcurved, stout, and broad, and has a slight hook on the tip. The rollers resemble crows in size and build, but are more glamorous and brightly colored, with patches of green, blue, violet, and brown. They are stoutly built perching and terrestrial birds of medium size (27 to 38 centimeters long) with large heads and plumed crests, short necks, short legs, rounded wings, a long tail, and syndactyl feet. The two inner front toes are connected, but not the outer ones. The coraciids include twelve living species and are found in the warmer part of the Old World.

Piciformes (Woodpeckers, Barbets, Jacamar, Puffbirds)

Several families of arboreal birds such as woodpeckers, barbets, jacamar, and puffbirds make up the order piciforms. Piciforms are tree-dwelling birds that nest in holes and have specialized bills, brilliantly colored feathers, and zygodactyl feet (two toes facing forward and two backward). In general, piciforms are insectivores, but the barbets and toucans eat fruits and honeyguides consume beeswax.

Stratigraphic range: Oligocene-Holocene; living species 387; length: 9–61 centimeters.

Trogonidae (Trogons)

Trogons are colorful forest dwellers distributed worldwide, but are more numerous in the Neotropics, Africa, and southern Asia, comprising twenty-nine species. They range in size from 23 to 40 centimeters. There is strong sexual dimorphism—male trogons have glittering green, blue, or violet heads and chests, with contrasting bright red, yellow, or orange body plumage to charm drab-looking females. They are arboreal and feed on insects and fruits. The wings are short and strong, but trogons do not fly often or for great distances.

Collidae (Mousebirds)

The collids, or mousebirds, are small, slender, grayish birds confined to sub-Saharan Africa that inhabit forest edges. These highly aerial acrobatic birds constitute a small family containing six living species, a surviving lineage that was more diverse in the Paleogene. They are small, gregarious birds about 30 centimeters long including a long stiff tail and a conspicuous crest and stubby bill; they often hang from branches and clamber through the leaves like rodents. They are arboreal and direct all four toes forward; they feed on fruits and vegetables. They are highly destructive, causing severe damage to fruit crops.

Strigidae (Owls)

The strigids, or owls, are raptorial birds that are found nearly worldwide. Most owls are solitary and nocturnal, and are cryptically colored in browns and grays for camouflage against a variety of backgrounds. They generally have round heads with flat faces, and many have feather ear tufts. They possess hooked beaks, strong talons, and soft, dense plumage that makes them virtually soundless in flight. The eyes are frontally placed, with a large component of binocular vision. When hunting at night, they use both sight and sound to detect prey. Owls often strike their prey with talons extended, often crushing their prey with their bills and tearing flesh with bills and claws combined. They swallow small prey whole, then they regurgitate bones, feathers, and fur in compact owl pellets. They have excellent hearing, and are especially sensitive to high-frequency, softer sounds. In darkness, they can detect the movements of small mammals on the woodland floor and quickly locate the source of the sound of potential prey.

The owls are divided into two groups: typical owls and barn owls. Typical owls are small to large nocturnal predatory birds with dark brown, gray, black, or reddish plumage and comprise 164 species. They are found on all continents except Antarctica. Their wingspans range from 30 to 132 centimeters. Bills and claws are strongly curved as in other falconiforms, and the females are larger than the males. Barn owls, closely related to typical owls, are nocturnal predators that subsist primarily on small mammals. They comprise seventeen species, and are widely distributed globally. Unlike typical owls, barn owls have a narrow skull behind a distinctly heart-shaped face. They are slim and of medium size with long, sparsely feathered legs and wingspans about 1.1 meters.

Stratigraphic range: Paleocene-Holocene; living species: 145; length: 13–69 centimeters.

Accipitridae (Hawks, Eagles, Kites, Harrier, Old World Vulture, Secretary Birds)

The accipitrids, the diverse diurnal raptors such as hawks, eagles, kites, the harrier, and the Old World vulture, are a family of small to large birds with strongly hooked and pointed bills, powerful feet, sharp talons, and keen eyesight. The eggshell looks greenish against the light. They range in size from the tiny South America's pearl kite, at about 15 centimeters long with a wingspan of 53 centimeters, to large eagles up to 1.5 meters long with a wingspan of about 2 meters. Most species are gray, brown, black, white, or a combination of these colors. Accipitrids are mostly terrestrial birds that soar magnificently overhead during the day, using thermals. Different groups within this family show different hunting techniques. Vultures and kites are primarily scavengers. The other accipitrids are strong fliers and pursue, capture, and kill their prey with their sharp talons in flight. They carry their prey with talons to a safe place and tear off flesh with their hooked bills for eating or feeding to nestlings. They hunt in forests and open woodlands and eat a wide variety of prey, including mammals, birds, reptiles, amphibians, fish, carrion, and many invertebrates. With 235 species, the Accipitridae is the largest family of the diurnal birds of prey and is found worldwide except for the polar regions.

The sagittarids, or secretary birds, are large, mostly terrestrial birds of prey that have quill-like feathers behind the head, a hooked beak, crane-like legs, and rounded wings. They are represented by a solitary species, *Sagittarius serpentarius*, confined to sub-Saharan Africa, mainly in Sudan and Saudi Arabia. They are large birds, weighing

from 2.3 to 4.5 kilograms; they stand almost 1.3 meters high, and their wings span 1.8 to 2.1 meters. Unlike most birds of prey, the secretary birds hunt their prey on foot. They stalk their prey in open country with long strides and then run in zigzag fashion after snakes, lizards, tortoises, and small birds and mammals. They usually strike their prey with one foot equipped with large claws. Normally terrestrial, they can fly well and can soar like a vulture or an eagle with their slotted wings and long central tail feathers.

Cathartidae (New World Vultures)

Traditionally, two major groups of carrion-feeders, the Old World vultures (Gypatinae) are grouped with hawks and eagles in accipitriforms, whereas New World vultures and condors (Cathartidae) are allied to storks and ibises within ciconiforms. Old World vultures differ from New World vultures in possessing strongly hooked feet, a rounded nasal opening, and a voice box. Vultures are large to massive birds with large slotted wings and possess excellent powers of soaring flight. They are bald-headed, devoid of normal feathers, which keeps their heads clean during carrion feeding. They are found on every continent except Australia and Antarctica.

Perhaps the most remarkable Ice Age vultures in the New World were the teratorns, such as *Teratornis* known from the La Brea tar pits of Los Angeles. This large bird stood some 0.75 meter tall and had a wingspan of 3.5 to 3.8 meters. Another record breaker was *Argentavis magnificens* from the Late Miocene of Argentina, weighing some 70 kilograms and having wingspan of 7 meters. *Argentavis* was the largest flying bird and exploited thermals for soaring across the Argentinean pampas for long-distance travel to detect prey from air. It was capable of catching sizeable prey with its formidable beak.

CARIAMIDAE, FALCONIDAE, PSITTACIDAE (Node N + Passeriformes)

Among Terrestriornithes, the radiation of modern land birds such as cariamids, falconids, psittaciforms, and passeriforms (songbirds) is the final episode of the diversification of Aves. By far the largest and most diverse group of living birds is the passeriforms that comprise 5,700 species, or nearly 60% of extant birds. The passeriforms have nearly always been placed at the crown of avian cladogram. But there has been persistent debate about their closest relatives. Recent molecular phylogeny suggests that psittacids (parrots) may be the closest sister group to passeriforms with falconids sister to this clade (node M). The parrots and songbirds are perching birds in which feet are specialized for grasping branches with strong claws. The foot of a passerine has three toes (numbers 2–4) directed forward and one enlarged toe (number 1) behind to grasp small branches, whereas in parrots, the feet are zygodactyl, where two toes (2 and 3) are directed forward and two toes (1 and 4) backward to improve the grip. It is generally believed that the zygodactyl foot gave rise to the anisodactyl foot of passerine birds.

Cariamidae (Seriemas)

The two seriemas species, the red-legged and black-legged seriemas, are the sole members of the family Cariamidae. They are large, long-legged terrestrial birds that range from 70 to 90 centimeters. They are grayish to brownish birds with hawk-like heads. They rarely fly, even if chased by predators. The red-legged seriema is larger and nests on the ground, but the black-legged seriema flies to a high roost at night. Like hoatzins, they are restricted to South America and are found in open habitats of grasslands, savanna, woodland, and forests of Brazil, Bolivia, Argentina, Paraguay, and Uruguay. They forage for small animals such as insects, frogs, lizards, snakes, and rodents. Cariamids are ancient birds. Several fossil forms such as *Salimia* and *Idiornis* from the Eocene Messel group of Germany and the gigantic flightless phorusrhacids such as *Andogaleornis* from the Pliocene of South America may belong to cariamids.

Falconidae (Falcons, Kestrels, Caracaras)

The falconids, the falcons and their allies such as kestrels and caracaras, are small to medium-sized birds of prey, ranging in size from 35 grams to 1.8 kilograms. They resemble the hawks and eagles in having hooked beaks, taloned feet, and keen sight, but differ in eggshell

color, which appears buff against the light. All species are mainly diurnal, though some small falcons such as hobbies hunt at dusk and the forest falcons hunt in complete darkness. There are sixty-four species in the family with a cosmopolitan distribution, except Antarctica.

Falcons are streamlined, diurnal raptors with long, pointed wings for high-speed acrobatic flight, where the wingspans range from 55 to 119 centimeters. They have sharp talons for grasping prey, and hooked beaks for killing and eating them. They hunt birds, small mammals, and insects by speed and stealth in the air. Because of the mid-air skill of these birds, falconry, in which pet falcons are trained to hunt and kill game, is one of the oldest sports in human history. The kestrel, a small falcon, is a familiar sight in American landscapes, perching on telephone wires. The peregrine falcon is legendary for its speed, reaching over 322 kilometers/hour, making it the fastest member of the animal kingdom. It hunts birds and bats in air by high-speed dives. In contrast, the carrion-feeding caracaras have rounded wings, feet adapted for walking, and a semibare face. They are small to medium-sized birds. They are strong fliers, and pursue and often capture prey on the wing. The family has a cosmopolitan distribution. They are carnivores, feeding on rodents, birds, reptiles, insects, and carrion. Within bird-of-prey species, there is a strong sexual dimorphism—the female is larger and heavier than the male. The birds of prey have sharp, hooked beaks with nostrils set into the fleshy cere and powerful feet with long, sharp talons and an opposable hind toe. In many ancient cultures falcons were worshiped as deities, as symbols of power.

Stratigraphic range: Upper Paleocene–Holocene; living species: 287; length: 15–150 centimeters.

Psittacidae (Parrots)

The psittacids, or parrots, comprise 372 species that are distributed in the Neotropics of South America, Africa, India, and Australia. They have long fascinated people because of their bright color, intelligence, ability to imitate human speech, and long lifespans. As a result, they are highly prized as pets. The parrots have a strong, hooked bill with a hinge on the upper part that permits great mobility of the upper beak during feeding. They are mainly seed- and fruit-eaters. They are highly social. They are stocky with a compact body, an upright stance, strong legs, and zygodactyl feet for grasping tree branches. Almost all parrots nest in the hollows of trees.

PASSERIFORMES (Node O)

The passeriforms are the dominant and most diverse groups of modern birds, comprising 5,700 species that are assigned to 1,161 genera and 110 families (Sibley and Monroe 1990). They are the second most species-rich order among vertebrates, after the perciform bony fish. The passeriforms are small perching birds, with feet adapted to cling to tree branches automatically. They are essentially landbirds and show great variation in size and color. They occur worldwide except in permanent ice and snow, and they occupy a diverse set of ecological niches. These are the most recently evolved birds with a high metabolism, a distinctive bony palate structure, and unique oil glands. They have relatively large brains and superior learning abilities, particularly with respect to vocalizations, which make them a highly intelligent group among all other birds.

Because the evolution of passerines has been rapid and relatively recent (since the Neogene period), and because of their small stature, morphological uniformity, and arboreal ecology, the fossil record is sketchy and has shed little light on our understanding of passerine relationships. The paucity of passerine fossils from the Early Tertiary led to the assumption that the group evolved later than most other modern families of birds (Feduccia 1996). The passeriforms apparently evolved out of a fairly close-knit clade of near-passerine birds such as the coraciiforms. Where and when did passeriforms originate? It is generally believed from fossil evidence that the origin of passeriforms occurred in the Oligocene or Miocene of Europe. Recent finds in Australia dating from the Eocene and later indicate that the passerines had a Southern Hemisphere distribution in the Early Tertiary (Boles 1997; Ericson et al. 2003). Molecular phylogeny confirms that the basal passerine group is the New Zealand wrens, the acanthisittids (Barker et al. 2004). The earliest split of the

basal group acanthisittids, or New Zealand wrens, from the rest of the passerine birds (the suboscines Tyranni and the oscines Passeri) supports the importance of former Gondwana continents in the early evolution of passerines. The Passeri, or oscine birds, probably emerged as the basal groups of corvoids and expanded deep into Eurasia and Africa, where there was a further explosive radiation of new lineages. Most passerine birds are small to medium-sized, but some are fairly large such as the Greenland raven.

Passeriform monophyly is well supported by both morphological and molecular evidence, but the interrelationships of the families and their composition within the order are highly controversial (fig. 11.10, node O). Currently, the passerines are divided into three clades, or suborders: Acanthisittidae, Tyranni, and Passeri (Sibley and Monroe 1990; Sibley and Ahlquist 1990; Barker et al. 2004; Ericson et al. 2003). The earliest radiation in the passerine tree is represented by the New Zealand wren family Acanthisittidae, which is the sister group of two other clades of passerines, the Tyranni (suboscines) and the Passeri (oscines). Fundamental differences in the anatomy of the syrinx distinguish two suborders of perching birds, the suboscines (Tyranni) and the oscines (Passers). The Tyranni, or the suboscines, have simple syrinxes and less complex vocal organs and their songs do not appear to be learned by imitation. The stapes of suboscines has a large bulbous footplate. They include tyrant flycatchers, antbirds, ovenbirds, and many diverse assemblages of the New World tropics. The suborder Passeri, or the oscines (songbirds), are characterized by a distinctive syrinx, or vocal organ, in their respiratory passage, and by associated complex vocalizations, which are learned through imitation. The oscines are responsible for most of the avian world's more melodic vocalizations and constitute about four-fifths of passerine birds. They are extremely uniform in morphology and include familiar temperate zone landbirds, such as robins, finches, thrushes, sparrows, warblers, cardinals, grosbeaks, and jays. Their middle ear bone, the stapes, is simple with a flat footplate.

Passerine birds have repeatedly evolved into convergent ecological forms that make the classification more difficult. A provisional working classification of major groups of passerine birds is listed below based on the recent understanding of the major patterns of their evolution (Sibley and Monroe 1990; Sibley and Ahlquist 1990; Barker et al. 2004; Ericson et al. 2003).

Order Passeriformes
- Suborder Acanthisitti (basal passerines)
- Acanthisittidae (New Zealand wrens)

The acanthisittids are very small (7.5 to 10 centimeters), greenish or brownish birds represented by four species, which are restricted to the forests of New Zealand. They have short, rounded wings, very short tails, long legs, and slender bills. They feed on insects, spiders, and occasional fruits. They lack the derived morphological traits used to define the two major clades of passerines, the oscines and suboscines. They are the evolutionary relics, the survivors of an ancient passerine lineage of a Gondwanan origin around 85 million years ago with no close living relatives (Sibley and Ahlquist 1990).

Suborder Tyranni (Suboscine Passerines)

Tyranni (suboscines) is a clade of passerine birds that typically inhabit tropical and subtropical regions in the New World, Africa, and Asia. They include about one thousand species of birds. Traditionally, suboscine families have included the broadbills and pittas of Africa and Asia and the asities of Madagascar. They also include two lineages of South American birds: woodcreepers, ovenbirds, antbirds, and tapaculos; and tyrant-flycatchers, cotingas, and manakins. The relationships among the suboscines have been a matter of considerable debate. Currently, the Tyranni contains two infraorders on the basis of geographic distribution: Eurylaimides (Old World suboscines), mainly distributed in tropical regions around the Indian Ocean; and Tyrannides (New World suboscines) from the Americas.

Infraorder Eurylaimides
- Eurylaimidae (broadbills)
- Philepittidae (asities)

Sapayoidae (broad-billed sapayoa)
Pittidae (pitas)

Infraorder Tyrannides
Furnariidae (ovenbirds and woodcreepers)
Thamnophilidae (antbirds)
Formicariidae (antthrushes)
Grallariidae (antpittas)
Rhinocryptidae (tapaculos)
Conopophagidae (gnateaters and gnatpittas)
Tyrannidae (tyrant flycatchers)
Tityridae (tityras, sharpbills)
Cotingidae (cotingas)
Pipridae (manakins)

Suborder Passeri (Songbirds or Oscine Passerines)

The Passeri, or oscine birds, include 4,500 species that show extreme morphological uniformity. They have more complex syrinx musculature and learn vocalizations from natural tutors. Most are small land birds primarily adapted for feeding insects, small fruits, and seeds. Sibley and Ahlquist (1990) grouped the oscines into two clades: Corvida (crow relatives), originating in the Austral-Papuan region; and Passerida (all other songbirds), originating in Afro-Asian region. Each is subdivided into three superfamilies and numerous families. The Corvida includes most of the families of the Australo-Papuan birds as well as crows, jays, drongos, shrikes, vangas, birds of paradise, and vireos. The Passerida includes assorted insect- and berry-eating songbirds such as mockingbirds and starlings, waxwings, chats, dippers, and the familiar thrushes, as well as insect-eaters such as nuthatches, titmice, wrens, swallows, warblers, and babblers. Although the oscine passerines constitute a monophyletic clade, its subsequent sister groups, named Corvida and Passerida (Sibley and Ahlquist 1990), have been found to be oversimplified and many novel classifications have been proposed in recent years to resolve the phylogeny of Passeri radiation. Most recent research suggests that Corvida appears to be a paraphyletic taxon within which the Passerida is nested, but the Passerida is probably a distinct clade (Barker et al. 2004; Ericson et al. 2003). Within the Corvida grade, there are three superfamilies, Menuroidea, Meliphagoidea, and Corvoidea, which are successive sister groups to all other oscines—the Passerida. There are a number of additional taxa not included in any superfamily.

Sibley and Ahlquist (1990) divided Passerida into three "superfamilies": Muscicapoidea (e.g., waxwings, dippers, thrushes, Old World flycatchers, starlings, and mockingbirds), Sylvioidea (e.g., nuthatches, tits, wrens, swallows, bulbuls, babblers, and sylvine babblers), and Passeroidea (e.g., larks, pipits, wagtails, waxbills, weavers, finches, sparrows, cardinals, tanagers, woodwarblers, and blackbirds). It has also been necessary to add a fourth, Certhioidea (Barker et al. 2004). Sylvoidea is sister to all other passeridans, and Muscicapoidea is sister to Certhioidea. Many of the recent classifications have rearranged the composition of the families within these three broad groups of Passerida (Barker et al. 2004; Ericson et al. 2003).

Suborder Passeri
Superfamily Menuroidea
Menuridae (lyrebirds)
Atrichornithidae (scrub birds)
Superfamily Meliphagoidea
Maluridae (fairy wrens, emu wrens, grass wrens)
Dasyornithidae (bristlebirds)
Meliphagoidae (honeyeaters)
Superfamily Corvoidea
Neosittidae (sitellas)
Vireonidae (vireos)
Ampephagidae (cuckoo shrikes and trillers)
Pachycephalidae (whistlers)
Oriolidae (orioles, fig bird)
Paramythiidae (berrypeckers)
Artamidae (wood swallows, butcher birds)
Malaconotidae (puff back shrikes)
Aegithinidae (ioras)
Prionopidae (helmet shrikes)
Vangidae (vangas)
Dicruridae (drongos)
Monarchidae (monarch flycatchers)

- Rhipiduridae (fantails)
- Paradisaeidae (birds of paradise)
- Coracoracidae (white-winged chough)
- Laniidae (shrikes)
- Corvidae (crows, ravens, jays)

Infraorder Passerida
- Superfamily Sylvioidea
  - Nicatoridae (nicators)
  - Panuridae (bearded reedling)
  - Alaudidae (larks)
  - Hirundinidae (swallows, martins)
  - Pnoepygidae (pygmy wren babblers)
  - Macrosphenidae (African warblers)
  - Phylloscopidae (leaf-warblers)
  - Aegithalidae (long-tailed tits)
  - Cettiidae (ground-warblers)
  - Locustellidae (grass-warblers)
  - Donacobiidae (black-caped donacobius)
  - Bernieridae (Malagasy warblers)
  - Acrocephalidae (marsh- and tree-warblers)
  - Pycnonotidae (bulbuls)
  - Cistiocolidae (cisticolas)
  - Timaliidae (tree babblers)
  - Pellorneidae (ground babblers)
  - Leiothrichidae (laughing thrushes)
  - Sylviidae (Sylvia warblers)
  - Zosteropidae (white eyes)
- Superfamily Certhioidea
  - Sittidae (nuthatches)
  - Certhiidae (treecreepers)
  - Troglodytidae (wrens)
  - Poliptilidae (gnatcatchers)
- Superfamily Muscicapoidea
  - Cinclidae (dippers)
  - Muscicapidae (Old World flycatchers)
  - Turdidae (thrushes)
  - Buphagidae (oxpeckers)
  - Sturnidae (starlings)
  - Mimidae (mockingbirds)
- Superfamily Passeroidea
  - Passeridae (sparrows)
  - Prunellidae (accentors)
  - Motacillidae (wagtails and pipits)
  - Estrildidae (estrildid finches)
  - Ploceidae (weavers)
  - Viduidae (indigobirds)

Classification of modern birds is a daunting task, which is slowly unraveling in recent years. Because of the relative conspicuousness of birds and the cues they use to recognize each other, birds are probably better known at the species level, but it is often difficult to classify them in higher ranks and establish their phylogenetic relationships. Current global diversity of birds results from processes that operate over both space and time and thus require an integrated approach using both morphological and molecular evidence.

The Explosive Evolution of Birds

With nearly ten thousand species of living species, birds are today's most diverse group of land vertebrates. Yet this number is only a small fraction of the number of species that have existed since the age of dinosaurs. The variety of birds is the acme of millions of years of evolutionary change and adaptation. This diversity is reflected most obviously in the varied and often brilliant plumage patterns seen in birds, not only in temperate parts, but also in a most spectacular way in tropical regions of the world. They live and breed in most terrestrial habitats and on all seven continents and fly wherever they want. Increasing discoveries of Cretaceous birds have revealed unexpected diversity of several lineages of ancient birds. The fossil record of modern birds improves greatly during the Early Tertiary period in both number of specimens and their completeness. Important levels of diversification of modern birds becomes apparent when fossil birds are compared on both sides of the Cretaceous-Tertiary (KT) boundary. The timing of the early radiation of modern birds is hotly debated: did orders of Aves evolve before or after the KT extinction event? Different models have been proposed to describe ordinal diversification before, near, or after the KT boundary. The fossil record may clarify this long-standing question.

Deciphering this evolutionary explosion of birds has been one of the major challenges for paleontologists for more than a century. The major problem is that for a long time our knowledge of Mesozoic birds was poor, known from few fossils. Recent discovery of extraordinary bird fossils from China, Mongolia, Spain, and Argentina has provided important clues about the tempo and mode of bird evolution. Our knowledge of the history of the evolution of birds begins in Texas, when an animal the size of a crow called *Protoavis* lived in the tropical forests of the American Southwest about 225 million years ago. Mastery of flight opened a world of ecological opportunities. At the time pterosaurs dominated the Mesozoic sky. Molecular evidence supports the Triassic origin of birds. From their humble beginning in the Late Triassic, birds diversified into a wide variety of overlapping clades during the Late Jurassic and Cretaceous periods represented by avialans, pygostylians, ornithuromorphans, enantiornithines, ornithurines, and avians. Early birds preferred an arboreal lifestyle for safety and food. As flight improved with the loss of the bony tail and modernization of the flight apparatus, many groups were capable of ground takeoff and explored a wide range of habitats. Some archaic birds ventured into water where food was abundant and became excellent swimmers and divers. Yet these early birds retained some primitive characteristics, such as clawed wings and teeth, though the latter was lost independently in a number of clades, including modern birds. During the Mesozoic evolution of birds, there was a major trend in the improvement of flight and the acquisition of skull kinesis. However, many groups of birds became secondarily flightless or reverted to a rigid skull configuration during this period. Recurrent reversals of flightlessness and akinesis have greatly altered the evolutionary trajectories of birds, modified their body plan, and complicated their genealogical history.

The discovery of *Polarornis* from the Maastrichtian deposits of Antarctica clearly suggests that early lineages of modern birds coexisted with the last dinosaurs. At least three modern orders of birds—palaeognaths, galliforms, and anseriforms—have been reported from the Late Cretaceous sediments that transcended the KT extinction and continued into the Cenozoic. Several recent studies of paleontological and molecular sequence data indicate that living lineages of modern birds (Aves) coexisted with other dinosaurs during the Late Cretaceous and passed through the KT extinction (Longrich et al. 2011; Dyke and Van Tuinen, 2004).

The KT extinction was a severe, global, and rapid extinction coinciding with twin impacts and massive Deccan volcanism and resulted in a major change in terrestrial ecosystems. Enantiornithes were the dominant landbirds in the Cretaceous, but coexisted with ornithuromorphs, ornithurines, and newly emergent avians or modern birds. The KT extinction wiped out the enantiornithine and basal ornithurine birds, but the handful of modern bird lineages passed unscathed through the apocalyptic cataclysm, and began to radiate explosively. The Cretaceous crisis was an important component in the radiation of birds. The explosive evolution of modern birds soon after the KT extinction from a small group of survivors is often regarded as a textbook example of adaptive radiation. Alan Feduccia (1995b) called this rapid diversification the "Big Bang" for Tertiary birds. It is a compelling story, but one where exact timing of radiation is important. The picture of adaptive radiation of birds is much more complex than the Big Bang model.

Overall bird diversity was low at first during the Triassic and Jurassic times. It appears that birds show three pulses of explosive evolutionary patterns, represented by Enantiornithes in the Cretaceous, Aves in the Tertiary, and Passeriformes in the Miocene (fig. 11.11). The turnover of avian lineages at three geologic periods is the result of successive bursts of adaptive radiation, multiplication of species through macroevolution, and extinction. Adaptive radiation is the rapid diversification of a single lineage into many species that inhabit a variety of environments or use a variety of resources and differ in traits required to exploit these. In other words, rapid evolution comes in bursts, with not just one new kind of bird appearing, but with many new kinds diverging from an ancestral group. To understand these three pulses of adaptive radiation of birds, we have to discuss macroevolution—evolution on a grand scale mediated by genomic

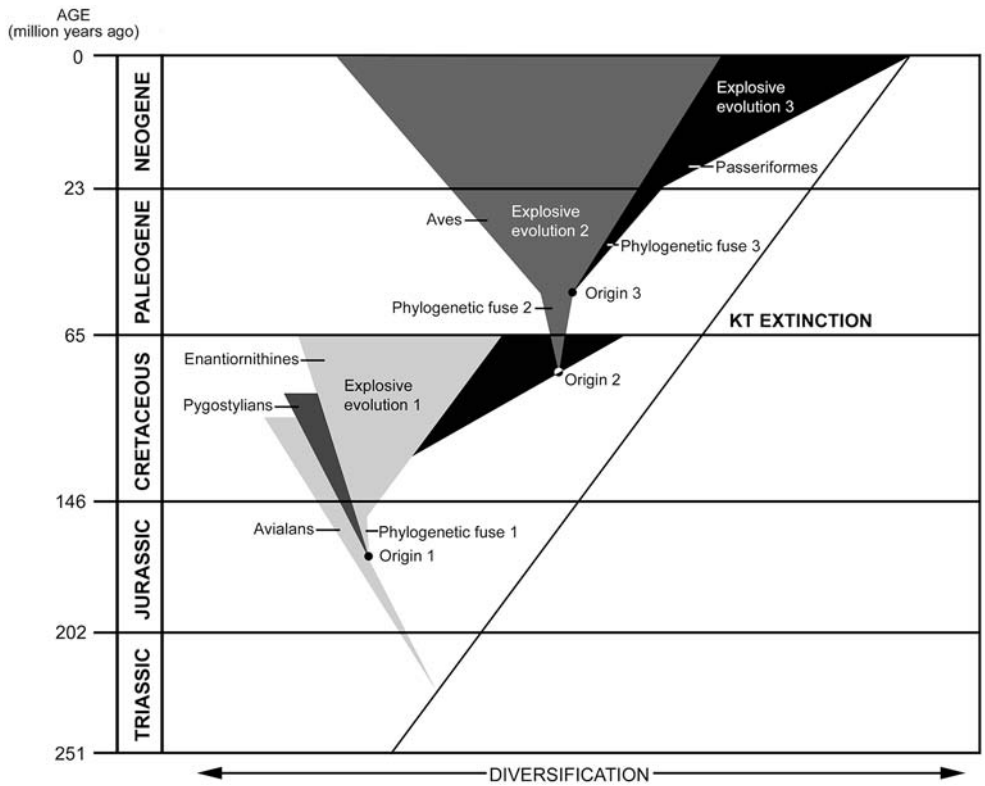


Figure 11.11. Macroevolutionary patterns of birds showing three stages: origin, phylogenetic fuse, and explosive evolution. There are three pulses of explosive radiations in birds: the first pulse is represented by the enantiornithine birds in the Early Cretaceous; the second pulse by the Aves, or modern birds, in the Early Eocene, which had a beginning in the Late Cretaceous; and the third pulse by the passerine birds in the Miocene. The origin of each clade is calibrated from ghost lineages.

enrichment when animals take giant leaps to exploit a plethora of available niches that lead to sudden species diversity and richness.

A Three-Geared Engine of Macroevolution

Macroevolution of major clades of vertebrates shows three distinct and successive regimes in ascending order on a timeline resembling a three-geared engine: (1) sudden "origin" of a higher clade by acquiring new genomes with a new ground body plan; (2) a prolonged period of stabilizing process called "phylogenetic fuse"; once the body plan was achieved, there was not much change; and (3) an "explosive evolution" and intense cladogenesis of the lineage (Chatterjee 2009). There appears to be extended time lags, perhaps millions of years, between intervals of these three macroevolutionary processes: origin, phylogenetic fuse, and explosive evolution.

What was the trigger for the macroevolutionary origin of birds? Most likely the macrogenesis event is a large-scale interspecific hybridization. Recent work suggests that hybridization is widespread in living birds leading to new speciation; about 10% of nonmarine species of birds regularly hybridize (Grant and Grant 1992). Hybridization, though a common mode of speciation in plants, is also increasingly implicated in the origin of a variety of animal species. Hybridization between species can allow alleles from one genetic background to integrate into another to form new gene pools if favored by selection and a new lineage, thus providing a key to quantum evolution among certain animal species. It confers several evolutionary advantages and represents a source of novel evolutionary trajectories. The extra genomes are thought to provide a buffering effect for deleterious alleles and gene mutations.

Why some lineages of birds such as enantiornithines, avians, and passerines underwent adaptive radiation is not well understood, but filling unoccupied ecological space appears to be a common feature. Ecological opportunity might arise as: (1) the colonization of new land or environments; (2) mass extinction of competitors and/or predators; (3) a new food resource; or (4) the appearance of novel evolutionary adaptations. As ecological and geological conditions change through time, they place varying demands on living bird species.

Three Pulses of Adaptive Radiation

Three pulses of adaptive radiation of birds reflect unique ecologic opportunity through geologic time. The first pulse of radiation is represented by enantiornithines in the Early Cretaceous. This early radiation might be linked to two factors: the fragmentation of Pangea with availability of new land environments, and novel body plan and evolutionary adaptations. Enatiornithines became considerably small, similar in size to many songbirds, and they became skilled fliers with a wide range of mobility and dispersal. They were perching birds with highly grasping feet and exploited different feeding strategies; they developed a large crop to store food. Since enantiornithine birds were highly diversified during the Early Cretaceous, their origin must have occurred during the Middle Jurassic or even earlier by inferring the presence of "ghost lineages" not documented by the fossil record but implied by the sister-group relationships of pygostylians and avialans (fig. 11.11). The enantiornithine birds died out at the KT extinction.

The second pulse of radiation of birds is represented by Aves in the Early Tertiary period, which is generally linked to the aftermath of the KT extinction event. It was the beginning of a new avian era. The fossil record of birds changes rapidly from the Late Cretaceous to Early Paleocene, with the loss of many groups of Cretaceous birds, most notably enantiornithines and some familiar groups of ornithurines such as hesperornithines and ichthyornithines. The Early Paleocene diversification of Aves began as a consequence of ecological voids left by the Cretaceous archaic birds and pterosaurs. However, true and rapid diversification of modern birds took place during the Paleocene-Eocene Thermal Maximum (PETM), about 56 million years ago. Few lineages of Aves were present in the Late Cretaceous but radiated dramatically during the PETM. This explosive evolution within 9 million years after the KT extinction produced most of the modern orders and families of birds.

Some of the spectacular Early Eocene bird fossils are preserved in the Green River Formation of Wyoming, London Clay of England, Messel Shales of Germany, and Quercy Phosphorite deposits of France. By the Eocene time virtually all major lineages of modern of birds had appeared except songbirds (passerines). These fossils include primitive representatives of frigatebirds, galliforms, perching birds, hawks, ibises, owls, swifts, woodpeckers, and rollers. Thus the crown clade Aves originated during the Maastrichtian, as revealed by *Polarornis* just before the KT boundary, which was followed by a long period of stasis, called phylogenetic fuse, which lasted for almost 10 million years, and then underwent explosive evolution during the Paleocene-Eocene boundary. The KT extinction left an impoverished avian fauna, but an evolutionary rebound during the Early Tertiary once again brought back biodiversity with full vigor. Life took several million years to recover. From this evolutionary bottleneck, birds underwent an explosive evolution in the beginning of the Tertiary, at the Paleocene-Eocene boundary as a result of ecological opportunity and favorable climatic conditions, diversifying and adapting to many different niches.

The third phase of explosive radiation produced more than five thousand species of passerine birds, the youngest of the neoavian clade that proliferated during the Miocene period about 23 million years ago. The widespread distribution of seed-bearing plants, especially the grasses and sedges in the Miocene, triggered the adaptive radiation of passerine birds with their wide range of beak morphology, smaller size, enlarged brain and intelligence, and vocal complexity. A particularly long hallux and a large hallux claw might have allowed them to be better at perching and foraging either arboreally or terrestrially than other small birds. The origin of passerines can be

calibrated from the oldest fossil record from the Eocene of Australia (about 55 million years ago). It was followed by a long period of phylogenetic fuse, until they became explosively evolved in the Early Miocene period (23 million years ago). High dispersal ability across the ocean barriers of passerines and their colonization on isolated islands might have influenced their rapid diversification process through allopatric speciation and hybridization. Passerine species multiply though hybridization and the geographical isolation of populations, which acquire new behavioral, ecological, and genetic characteristics.

12 The Origin of Flight

A bird flies according to mathematical law, which is within the capacity of man to reproduce with all its movements.

Leonardo da Vinci, *Codex on the Flight of Birds*, 1505

The Miracle of Flight

Birds are versatile fliers among vertebrates because of their lightweight and streamlined bodies, feathered wings, and powerful flight muscles. The evolution of flight in birds is generally recognized as the key adaptive breakthrough that took them to a new aerial world above the realm of the terrestrial dinosaurs. The low expenditure of energy required for flying relative to that needed for walking or running made early birds more mobile than earth-bound dinosaurs. Flight allowed birds to escape from predators on the ground, to exploit new resources, to nest in trees, to search for mates, to migrate rapidly to more favorable habitat, and to exploit the best seasons for reproduction and survival.

From time immemorial humans have watched and envied the enchanting flight of birds, whose aerial freedom they wanted to emulate. Many believed flying was reserved for mythical gods and angels. But birds were an ever-present reminder to man that gravity could be defied, that he, too, might fly if he could unlock their secrets. This prospect of conquering the air fascinated him. He tried to imitate bird flight unsuccessfully by jumping from cliffs before finally realizing that the human body was not designed for flight. Undaunted by structural deficiencies, early inventors dreamed up ideas for flying machines and mimicked the design of birds in hopes of achieving the freedom of flight. Many flapping and gliding contraptions were conceived and tested—endeavors that yielded not only a sense of disappointment and casualties, but also insights about flight dynamics. Humans have neither the required muscle strength to fly nor the ability of birds to control wing configuration required to develop necessary lift and thrust for flight.

During the Italian Renaissance, Leonardo da Vinci studied the anatomy and physiology of birds, their wings, their musculature, and their feathers. He was the first to record the scientific study of aeronautics and experimented to prove the feasibility of biomechanical flight. He developed concepts of the propeller, the parachute, and heavier-than-air craft. In a collection of notebooks, *Codex on the Flight of Birds*, da Vinci described his dreams and inventions for human flight, including a pair of self-propelled

flapping wings and the Ornithopter, a mechanical flying machine with flexible wings. Da Vinci knew that any flier needs an upward force, or lift, to counterbalance its weight, and by far the most economical way to produce lift is to use wings. The flight of fancy was realized after the trials and tribulations of many pioneers. During the past few centuries men like da Vinci, George Caley, Otto Lilienthal, Samuel Langley, and the Wright brothers kept careful notes and diaries on their observations of birds during their pursuit of artificial flight and developed the theory of aerodynamics. From birds they learned the basic elements of wing design and realized that control or maintaining balance in unstable air is the most critical aspect of sustained flight. Manned flight, like avian flight, evolved through successive stages—first parachutes, then gliders, and finally true flying machines.

The beginning of the twentieth century heralded the age of aviation. On December 17, 1903, Orville Wright, assisted by his brother Wilbur, made the first historic flights over Kitty Hawk, North Carolina, with their *Flyer* biplane and proved once and for all that humans could fly like birds across mountains and oceans. World War I sped up aviation technology with the improved design of engines to enhance speed and loads. Paradoxically, it was the human's own inventions—first the glider and then the powered airplane—that were the keys to recognizing the secrets of avian flight.

How do birds fly so gracefully? Birds fly in air by flapping their wings to produce thrust as well as lift, while steering mainly with their tails. Most of the surface areas of bird's wings are made of feathers, which are internally reinforced by the bony frames of the forelimbs. The flight performance of a bird depends on a number of factors: wing size, airspeed, air density, and the angle of the wings with respect to the direction of flight. A bird moving through the air experiences an aerodynamic force that retards its motion—resistance, or drag, which is proportional to air density. In both airplanes and birds, the body is streamlined to reduce drag forces. Flight is a combination of lift and propulsion. Like airplanes, all flying animals are heavier than air and require a lift force to keep them aloft. For a wing to make lift, it must deflect air downward. So as it moves through the air, a wing pushes air down; the air pushes back with an equal and opposite reaction to produce lift. In an airplane, the wings are metal-skinned and fixed to provide lift, while the engine gives the forward thrust. In birds, the wings are inherently dynamic and flexible to provide both lift and thrust, and their geometry can be changed in response to flight. Birds can morph their wings, change their size and shape, move them up or down, forward or backward, or twist or bend them; the feathers of the tip of a wing can be spread or closed.

Bird flight is a complex performance of wing movements, aided by an equally complex set of moment-by-moment body and tail adjustments to provide balance and control. Birds flap their wings with powerful flight muscles. Besides the up-and-down motion, another key motion is rotation of the wing around its long axis—tilting the leading edge up or down. In flapping motion, the downstroke is the power stroke. On the downstroke, the wing moves down and forward, producing both lift and thrust. The upstroke is mainly a recovery stroke that produces little or no thrust or lift. In birds, each wing functions as a combined wing and propeller. During the downstroke, the inner wing is tilted leading edge up to supply most of the lift, while the outer wing is twisted leading edge down to serve as a propeller to produce thrust. The tips of the bird's wings not only flap up and down but also twist forward on the downstroke. This twisting motion of the wing propels the bird forward, while flight muscles provide the power (fig. 12.1). In both birds and aircraft, wings need to be strong enough to carry the fliers' aerodynamic load. In airplanes, the cockpit is the command post for flight; in birds, the brain controls the complex neuromuscular movement; their nervous systems are superbly integrated and adapted to operate their flight systems in a direct and intimate fashion that human pilots can only envy.

In flight, aircraft face aerodynamic problems similar to those of birds and engineers have arrived at remarkably similar solutions. Propellers, wings, flaps, and stabilizers all have equivalents in birds. Birds have evolved many marvelous devices to enhance their performance

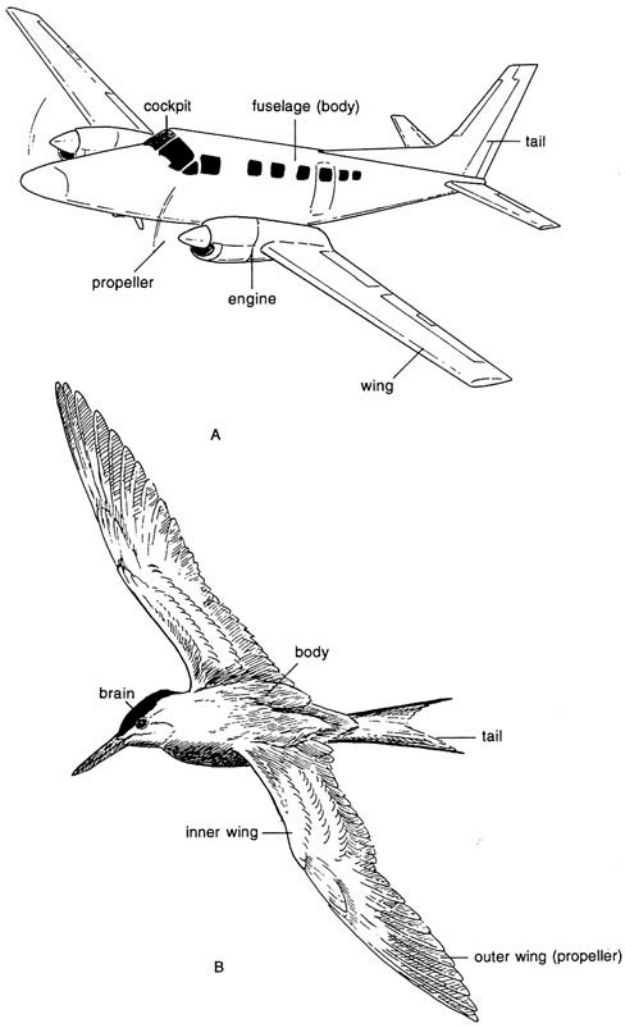


Figure 12.1. Comparison between a propeller airplane and a bird. A, in an airplane, the wing provides the lift; the propeller, powered by the engine, gives the forward thrust; and the cockpit is the controlling system. B, in a bird, the wing functions as both a lifting surface and a propeller; the inner wing supplies most of the lift, the outer wing serves as a propeller, and the brain controls the complex neuromuscular movement (proprioception) of the wing. In both cases, the tail provides stability and has an important function in controlling flight, steering, and braking. Bodies are streamlined and landing gears are tucked close to the body during flight to reduce drag but are lowered during landing (after Chatterjee 1997).

and to adapt to their particular lifestyles. Early aircraft designers have mimicked, usually inadvertently, many avian flight "inventions," such as the basic airfoil shape of the wing and streamlining of the body; ailerons for aerial turns comparable to the differential twisting and banking of the wings along the rolling axis; leading-edge slats to delay stalling, as does the alula of birds; a gyroscope to sense orientation in flight analogous to the vestibular system of the inner ear; airbrakes and extension of the trailing edges (flaps down) to increase the wing area and camber when approaching landing similar to the extension of avian feet, thus preserving lift at slow speeds necessary for a smooth touchdown; elevators like tail feathers to control the pitch; and landing gear that imitates the retraction of a bird's feet when in flight (Chatterjee and Templin 2007).

Other avian characteristics, such as morphing wings and perching, were more difficult to copy. The wings of an airplane are fixed with respect to the fuselage. In contrast, bird wings are flexible with sophisticated multihinge joints that can be flexed and extended at the shoulder, elbow, and wrist to alter the wingspan and change the camber and angle of attack. Birds may have camber as high as 15%. They use a good deal of camber in the downstroke and reduce or eliminate it in the upstroke. High camber is useful in some conditions, particularly at low speeds. Drag increases with the degree of the camber. During cruising flight, a bird decreases the camber, while during pitching and hovering it increases its camber to stall forward movement. In aerial turns a bird beats one wing faster than the other. Birds use their wings in different manners in various types of flight—ascending, descending, horizontal, hovering, flapping, and soaring.

Birds' wings, with their sharp leading edges and textured surfaces, are quite different from aircraft wings. Birds can change the shape of their wings, which are frequently deformed during flapping. They shorten their wingspan by drawing their wings toward the body during the upstroke and extending their wings during the downstroke. Morphing wings allow birds to change the shape of their wings to suit the needs of their mission. Birds are much more precise in landing on a branch than aircraft landing on a runway. They increase the angle of attack of their wings until they stall, spread and lower their tails, and extend their legs and feet as brakes. Finally, the self-renewal mechanism of wings in birds has no parallel in man-made machines. Engineers have not managed to

build wings or any other structures that can make their own repairs.

To allow birds to deftly maneuver between trees and other obstacles, the flight mechanism has to be more versatile and complex than that of an airplane. Engineers adopted a different path to build powered aircraft for speed, efficiency, stability, safety, and automation from that taken by birds because of scale differences. As a result there was little technology transfer from birds to aircraft design once the basic aerodynamics of wings were adopted. An airplane must be far larger and heavier than the biggest flying birds for carrying engines, loads, and passengers and must fly much faster than birds just to stay airborne. After learning the secret of flight from birds, designers of modern aircrafts began to deviate from avian design to meet the demands of defense, human comfort, and commerce with the adoption of jet engines and computerized technologies, which help to extend the human domination of this planet and beyond to the Solar System.

Flight Styles

Flight differs from other kinds of locomotion in that the weight is supported by an aerodynamic lift force, compared to walking or running (the weight is supported by gravitational forces on the ground) or swimming (the weight is supported by hydrostatic forces in water). Flight defies the laws of gravity by using aerodynamic forces. The wing of a bird is constructed on sound aerodynamic principles. A flying bird generates lift forces to counteract gravity and thrust forces to overcome drag. A bird's wing is slightly curved from front to back, producing an airfoil profile in which the trailing edge comes to a sharp point rather than a blunt edge, a feature that greatly improves lift production. Forces created by the flow of air over the wings keep a bird airborne. The asymmetric flight feathers are attached to the outer wing to produce the twist or wing warping at the tips needed to generate thrust. The thumb, attached to the front of the hand section, just beyond the wrist, is the alular wing that helps birds fly well at lower speeds, such as during takeoff and landing. The spanwise lengthening of the wings is the most obvious adaptation to flight. Birds acquired the long span not only by the lengthening of the forelimb bones, but also by extension of the long primary feathers beyond the rigid tips of the fingers.

Birds have developed different styles of flight such as gliding, soaring, hovering, and flapping, reflected by the size and shape of the wings. Each bird has wings that best fit its way of life. There are basically four major types of wings (fig. 12.2): elliptical, high-speed, high-aspect ratio, and slotted high-lift. Elliptical wings are short and rounded and are suited for maneuvering through the forest canopy. They are found in woodpeckers, jays, magpies, and hornbills. Such wings have a low aspect ratio and a somewhat reduced tip vortex that facilitate darting and turning quickly. High-speed wings are short and pointed and are characteristic of birds that feed on the wing or make long migrations. These wings are built for speed. They have a low camber and fairly high aspect ratio and are found in shorebirds, swifts, hummingbirds, and swallows that flap their wings as they chase insects in the air. High-aspect ratio wings, most commonly found in seabirds such as albatrosses and frigatebirds, are long, narrow, flat, and pointed with no slotting of the primary feathers; they enable soaring in open spaces while riding on the wind. These wings are adapted for long-distance soaring over the ocean using the differential wind velocities at different heights (wind shear) or thermal currents so that birds can glide endlessly above the sea. The slotted high-lift wing is the fourth type, found in the larger species of terrestrial soaring predators such as eagles, hawks, vultures, owls, pelicans, and storks that soar more slowly over lands using thermals; these birds carry prey to their nests using their legs, which are streamlined with long contour feathers attached to the tibia. These wings have moderate aspect ratio, deep camber, and slots at the tips and between the primaries to reduce drag. Some birds developed mufflers in their wings for stealth and silence for catching prey. For example, in night fliers such as owls, the wings have soft feathers across the surfaces that muffle the noises made by flapping. This helps an owl approach its prey without being heard.

The tail section of a bird completes the streamlined shape of the body during cruising flight when the tail

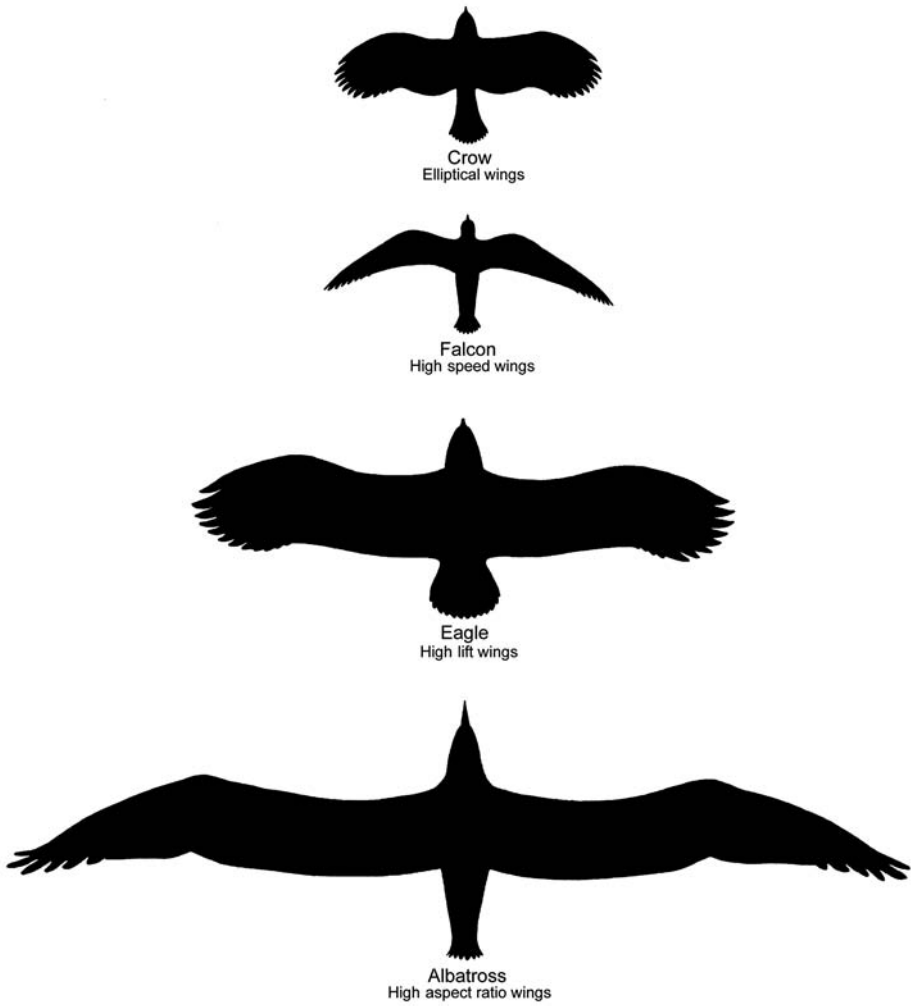


Figure 12.2. Wing shape and flight. Bird wings can be broadly grouped into four types: short and rounded elliptical wings for tight maneuvering; short and pointed high-speed wings with heavy wing loading and rapid wingbeats; slotted high-lift wings for thermal soaring; and long and pointed high-aspect ratio wings for gliding and dynamic soaring.

feathers are folded. Most birds have short triangular tails when spread from the pygostyle to form an effective airfoil. Birds use their tails as flight apparatus in concert with their wings for correction of small errors in pitch and yaw, maintaining lift at low speeds, and enhancing maneuverability. The tail of a bird can be used to coordinate a turn or employed as a flap to increase camber of the flight surfaces. The tail is quite active as an elevator to control the pitch and angle of attack, particularly during takeoff and landing. If the tail is depressed, the head pitches upward to produce greater lift at a higher angle of attack during takeoff; when the tail is raised, the head points downward with a consequent decrease in the angle of attack, which reduces lift during landing. The tail is used as a vertical stabilizer as well as a rudder in birds. During steady level flight, the tail provides stability for the bird, to keep it flying straight. Unlike the fixed wing stabilizer, the tail of a bird is flexible and can function like the rudder of an aircraft to control the head of the bird. When a bird takes aerial turns by banking and flapping its wings unequally, an unbalanced side force component is generated. The twisted tail ensures that the bird is properly aligned to the curved flight path during maneuver. In flight, the tail is influenced by the time-varying wake of

flapping wings and the flow of air over the body. Various movements of the tail—raising, lowering, twisting, opening, and closing—help the wings in supporting, balancing, steering, and braking the body in flight.

The wings are the primary devices for flight while the hindlimbs remain passive. During steady level flight the legs and feet are tucked neatly into their undertail coverts to reduce drag, but when taking off, when changing direction, when sudden gusts of wind are encountered, or when landing, the legs and feet have important steering and balancing functions. They act as retractable landing gear and play crucial roles during takeoff and landing.

Birds fly in a variety of ways, ranging from gliding to soaring to flapping to hovering. The flight styles can be grouped into three categories on the basis of size and wing design: small birds are capable of hovering flight, medium-sized birds are built for flapping flight, and large birds use gliding and soaring flight. The size of a bird may be related to lift-to-drag ratios. Flight performance seems to degrade systematically with increasing body size from hovering to flapping to soaring because power decreases with body size. Above a particular size, the available power is insufficient and flapping flight is not possible except during takeoff and landing. Side by side, there is a regular progression and improvement in gliding performance in birds from small to large species; the lift-to-drag ratio increases from 4 in small birds such as sparrows to 19 in large birds such as wandering albatrosses.

The Mechanism of Flight

Birds have evolved many marvelous devices to enhance their performance and to adapt to their particular lifestyles. Some of these devices are mimicked in aircraft design, which can be studied from aerodynamic principles, but some are unique to birds and are highly complex. The basics of flight performance can be studied from wing design. Bird wings need to be as light as possible for both ease of flapping and efficient flight, while still being strong enough to support the animal's weight in flight. The air in which birds fly is a gas or fluid, which is a substance without a shape of its own, consisting of moving particles. The air deforms easily under the slightest pressure and fills any space completely. Air, like water, has weight and exerts pressure. By taking advantage of these properties, both birds and aircrafts can maintain themselves in the air. When a bird flies, it is subjected to gravity and drag. Gravity produces weight, which is a vertical force in a downward direction. Movement of air over the wings provides the lift to overcome the force of gravity, raise the bird into the air, and keep it there. The wings produce lift, the upward force, which is perpendicular to the movement of the wing. Birds that are flying forward must drive air both downward (for weight support) and backward (for thrust) to produce opposing forces.

Moving air has properties that differ from those of static air, for as soon as an object and air start moving in relation to each other, another force—drag—begins to exert its influence. Unlike lift, drag is a horizontal force, which is produced when a bird moves forward; drag slows the bird down. Drag is generated when a solid object moves through a fluid medium. Drag increases with velocity—the faster an object travels, the more drag it experiences. Any force in the opposite direction of drag is thrust that keeps the bird flying forward. The total drag in a flying bird involves more than the wings. Drag varies with air density and the total surface area, shape, weight, and speed of the flying bird. Like lift, drag is proportional to dynamic pressure on the area on which it acts. There are three major drag forces that impede a bird's aerial flight: frictional drag caused by the friction of air and body surfaces; pressure drag due to the frontal area of the bird; and lift-induced drag caused by the wingtip vortices. The wing's thin leading edge minimizes frictional drag; streamlining and the narrow cross section of the body reduce pressure drag (see the discussion below on the streamlined body); and various wing shapes reduce induced drag.

Induced drag occurs when the airflow separates from the surface of the wing. As wings move through the air, air is moved from an area of high pressure (under the wing) to an area of low pressure (on top of the wing); this curling action causes spirals (vortices) of air, which can disrupt the smooth airflow over the wing and reduce lift. Some wing shapes help to reduce induced drag. Two pat-

terns of vortex wake have been observed during flapping flight: leading-edge vortex and wingtip vortex (Alexander 1983). During slow flight in short-winged birds, the leading edge vortices form rings after each downstroke, like a series of smoke rings. As air passes below the sharp leading edge of a bird wing, it curls up over the trailing edge, drawn there by low pressure on top. Leading-edge vortex is a region of low pressure above the wing, and this provides extra suction that increases lift during slow motion. During fast motion in long-winged birds, the wingtip vortex streams the wings continuously, forming an undulatory cylinder trailing behind each wingtip. A tip vortex not only causes drag and destroys lift at the tip alone; it also spills over the upper wing surface and interferes with the airflow there. To keep this interference as low as possible, many bird wings have narrow and pointed wingtips that minimize pressure differences and therefore turbulence at the tip. Similarly, the feathers that form slotted wings reduce induced drag by acting as winglets that spread vorticity both horizontally and vertically.

When a bird is in level flight in still air with no flapping of the wings, four forces—lift, weight, thrust, and drag—are equal and opposite (fig. 12.3A). Weight acting downward under the pull of gravity is balanced by lift generated by the wing. If the lift is greater than the weight, the bird will rise; if they are equal, the bird will fly at constant altitude; and if the lift is less than the weight (as in gliding), the bird will descend. If a bird wants to fly at constant height and speed, the lift acting on it must be equal to its weight, while the drag must be equal to the thrust. Similarly, the resisting force of drag equalizes the forward thrust provided by the wingtip. Drag has a direct effect on acceleration. As a bird accelerates, its velocity and drag increase, eventually to a point where drag becomes equal to thrust—in which case no further acceleration can occur. Drag is dependent on the shape or morphology of the bird, but independent of its size, and is often measured by a parameter called the drag coefficient. A bird can increase or decrease drag by morphing its wings to accelerate or decelerate. In order to maintain steady horizontal flight, thrust must be greater than drag, or the bird will decelerate until it stalls.

Gliding is passive flight without wing strokes; it requires a minimum of energy. In gliding, lift balances weight but drag remains uncompensated (fig. 12.3C). As a result, the animal must descend. In flapping flight, the thrust generated by wing strokes balances drag (fig. 12.3B). Flapping, or powered, flight is much cheaper locomotion than is running (Rayner 1991). Changes in lift or thrust cause birds to change speed and altitude. A flying animal must overcome the force of gravity by generating vertical lift and producing horizontal thrust to counter drag. Lift is produced by the inner part of the wing, where the wing area is largest, whereas thrust is produced by twisting the outer part of the wing.

Functions of Wings

The shape and size of wings determine the flight pattern and lifestyle of birds. Two features of wings are linked to flight performance: the aspect ratio and wing loading (fig. 12.4). These two quantities are widely used both in aircraft engineering and in studies of bird flight. To fly economically, the wings must be slender. The slenderness of the wings can be measured by the *aspect ratio*—the ratio of the wingspan to wing width or chord (fig. 12.4A). For most wings the length of the chord is not constant but varies along the wing, so the aspect ratio (AR) is defined as the square of the wingspan (b) divided by the wing area (S) of the wing planform; so $AR = b^2/S$. It is a dimensionless index of the shape of the wing, being high for a long narrow wing and low for a short broad one. The average value is 7, with a range from around 4.5 in some galliforms to as high as 19 in albatrosses.

Birds with long, narrow wings, such as gulls and albatrosses, have a high aspect ratio and a high lift-to-drag ratio. The long wing is structurally weak but is aerodynamically efficient for gliding and soaring. Long wings are, therefore, most suitable to birds that live in open airspace. Flight is cheap for these long-winged birds, as it requires little muscular effort, but takeoff is difficult. For example, frigatebirds cannot take off from the ground but need a perch. Birds of prey also have developed wings of high aspect ratio; their wings taper to a point and tend to be swept backward. Wings of harriers and vultures are

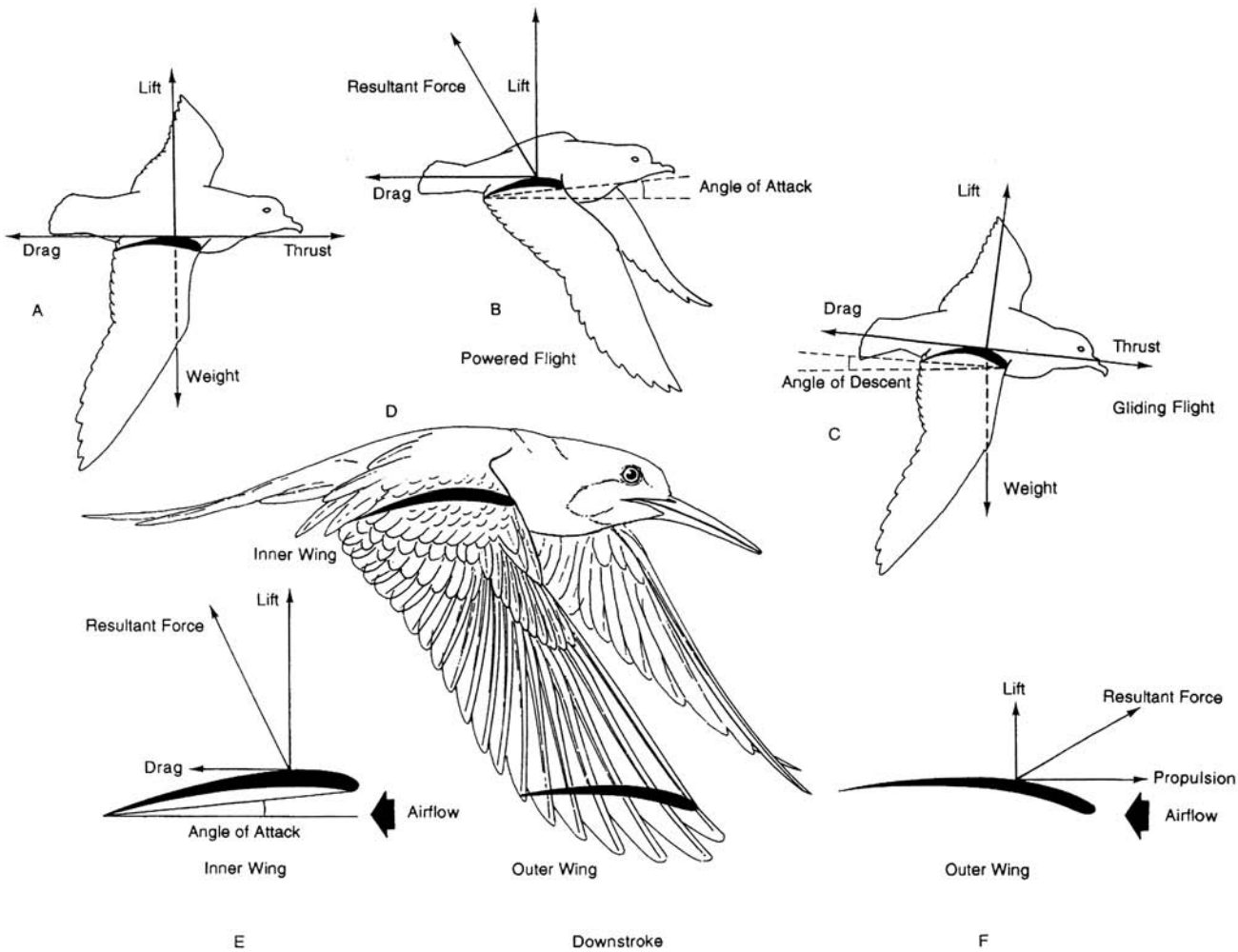


Figure 12.3. The biomechanics of flight. A, when a bird is in level flight, four forces (lift, weight, thrust, and drag) are equal and opposite. Changes in lift or thrust cause the bird to change altitude or speed. B, the bird's wings act as an airfoil in powered flight. The airflow over an airfoil generates the forces of lift and drag. The flying wing maximizes lift and minimizes drag. The angle between the airfoil and the airflow is called the angle of attack. As the angle of attack increases, lift becomes greater than drag, and the resultant flight is more vertical than horizontal. C, in gliding flight, the airfoil of the wing provides the lift, while the pull of gravity is used as the thrust. Gliding is always accompanied by loss in height with an angle of descent of less than 45°. D, airfoil cross sections of the inner and outer wings of a bird during the downstroke in relation to the direction of airflow. E, the inner wing provides lift as the angle of attack is about 5°. F, the outer wing is twisted and tilted downward in relation to the direction of the airflow, so that the airfoil creates a forward thrust, or propulsion (after Chatterjee 1997).

relatively broad, with slotting of the primary feathers, which are adapted for soaring in thermals and for precise control in the pursuit of prey.

Birds living in woodland habitats would find long wings a handicap and thus evolved elliptical wings. Short, broad wings with a low aspect ratio provide rapid, powered lift and maneuverability through the forest canopy. Most fast fliers designed for sophisticated acrobatics, such as swifts and pigeons, possess short, wide wings with a low aspect ratio and a low lift-to-drag ratio. As a result, such birds have to flap their wings continuously to remain aloft. Flight is expensive for these groups of birds.

Weight is another important factor in flying performance. Weight (W) is often confused with body mass (M). However, weight is the product of mass and gravitational acceleration ($W = Mg$; $g = 9.81\ m/s^2$) and is often

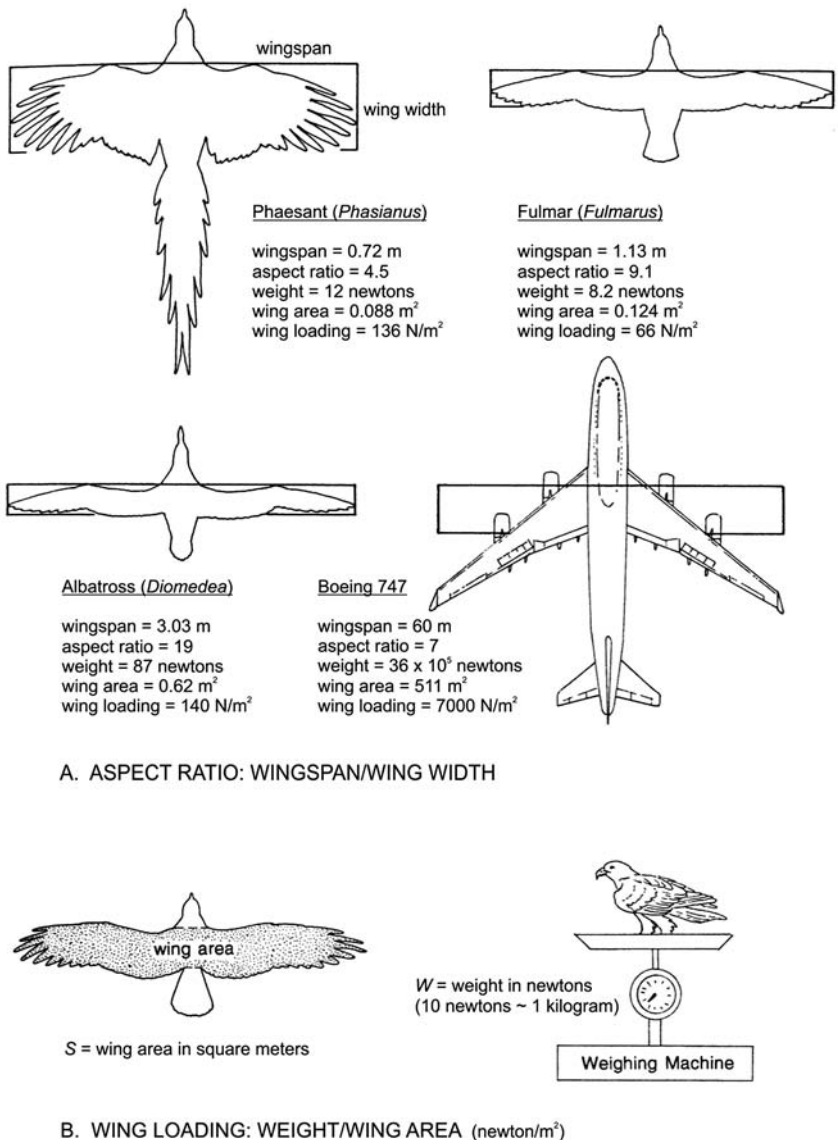

wingspan
wing width
Phaesant (Phasianus)
wingspan = 0.72 m
aspect ratio = 4.5
weight = 12 newtons
wing area = 0.088 m²
wing loading = 136 N/m²
Fulmar (Fulmarus)
wingspan = 1.13 m
aspect ratio = 9.1
weight = 8.2 newtons
wing area = 0.124 m²
wing loading = 66 N/m²
Albatross (Diomedea)
wingspan = 3.03 m
aspect ratio = 19
weight = 87 newtons
wing area = 0.62 m²
wing loading = 140 N/m²
Boeing 747
wingspan = 60 m
aspect ratio = 7
weight = 36 x 10⁵ newtons
wing area = 511 m²
wing loading = 7000 N/m²
A. ASPECT RATIO: WINGSPAN/WING WIDTH
wing area
S = wing area in square meters
W = weight in newtons
(10 newtons ~ 1 kilogram)
Weighing Machine
B. WING LOADING: WEIGHT/WING AREA (newton/m²)

Figure 12.4. Wing shape, wing size, body weight, and flight style of birds compared with those of a Boeing 747. The wing shape of birds reflects the way in which they live, particularly the ratio of wingspan to wing width, known as the aspect ratio. A, comparisons of aspect ratios of different birds and the Boeing 747. B, wing loading is the ratio of total weight to wing area (after Chatterjee 1997; aerodynamic data from Tennekes 1996).

expressed in newtons (N). For example, if the body mass of an albatross is 10 kilograms, its weight is 98.1 newtons.

Wing loading is an important parameter that affects the performance of a flying animal. It is a measurement of how much total weight is supported by how large a wing. Wing loading (*WL*) is the ratio of the bird's weight (*W*) to the wing area (*S*) (fig. 12.4B). Thus $WL = W/S$ or Mg/S. Unlike aspect ratio, which is a dimensionless quantity, wing loading is often expressed as newtons per square meter (N/m^2). It also varies with size, tending to be larger in larger birds. It ranges from 18 in a small hummingbird to 70 in a California condor. Flying speed in flapping and gliding flight is approximately proportional to the square root of the wing loading. Larger animals (and aircraft) not only have higher wing loading but also faster speeds than do small ones. Small birds with a low wing loading are

more maneuverable than are large birds with a high wing loading; the latter have to fly faster to generate the lift required to stay airborne. A Boeing 747 flies much faster than a sparrow because of its high wing loading (Tennekes 1996).

Requirements for Flight

There are four basic requirements for flight: a lightweight and streamlined body, the production of lift, power or thrust, and a control system. These adaptations are centered on two prime demands for any flying machine: high power and low weight. These requirements are described below.

A Lightweight and Streamlined Body

A Lightweight Body

A major structural requirement for flight is a light, yet sturdy skeleton, combining lightness with strength. Birds became lightweight by reducing their size and evolving thin, hollow, pneumatic bones. Lightweight bodies help birds to be good fliers. The less weight a bird has to lift, the more easily it can fly. Birds have light, delicate, and hollow bones laced with air cavities and stiffened with struts to form an effective airframe. Bird bones are not only light but also strong, reinforced with an internal crisscrossing strut system that provides strength and stability to withstand the heavy strains of flight. The skull is also made of paper-thin sheets of bone, fused together and stiffened inside with thin rods. The heavy jaws with teeth of protobirds were replaced with a lightweight beak covered with a horny sheath. The neck is flexible so that birds can reach any part of their bodies with their beaks. The breastbone, though extremely light, has a deep keel, which not only makes it rigid, but more important, provides a large surface area for attachment of a pair of powerful flight muscles—the pectoralis and supracoracoideus. The furcula, made up of fused collarbones, is reduced to a flexible spring between the shoulder bones that aids in flight during flapping. Sturdy construction of the flight apparatus resists the compressive force of the wings during flight. The bones of the hands are fused and reduced to support the flight feathers. The hindlimbs are modified into landing gear. The tall and elongated pelvic bones and sacral spines are all fused to create a sturdy platform, the synsacrum, which reduces weight, shifts the center of gravity over the feet during walking, and provides strength and rigidity to withstand the impact of landing. The long, theropod-like bony tail that early birds inherited has been reduced to a small plate, the pygostyle, at the end of the hips. Birds have eliminated several structures to reduce their weight such as most skin glands, a long bony tail, and some digits.

Bird bones are pneumatic, which means that hollow air spaces within the bones are directly connected to the respiratory system, enhancing respiratory efficiency. Since birds do not possess a diaphragm muscle, as found in mammals, how do they regulate airflow during flight? Birds have a unique and efficient way of breathing by expanding their air sacs, not by expanding their lungs. The lungs are small and relatively less flexible, but they are interconnected with a system of bellows, or flexible air sacs (usually nine in number), which help ventilate the lungs. Birds actually breathe in twice to complete one full respiration. When a bird inhales, the air first passes to its lungs. It then continues through a number of small tubes into air sacs that lie toward the rear of the body. When the bird breathes out, the air in the rear sacs moves back along other sets of tubes to a different part of the lungs. On the second inhalation, air in the lungs, depleted in oxygen and full of carbon dioxide, flows from the lungs to the anterior air sacs, while fresh airs flows down bronchi to the posterior sacs once more. On the second exhalation, the stale air is pushed up from the anterior air sacs out of the bird. The air sacs permit a unidirectional flow of air through the lungs, where gases are exchanged between the lungs and the blood in the parabronchi. These complex air sacs and interconnecting tubes have important connections with the skeleton that help cool the body during flight. Unlike the mammalian diaphragm, the air sacs in birds are pumped by the action of hinged ribs and the furcula. The uncinate processes of the thoracic ribs in birds are crucial ventilatory structures, involved in both inspiration and expiration. Most likely there is a fine coordination between flight stroke and respiration as revealed from the

dorsoventral movement of the sternum and the furcula during each wingbeat, which may assist airflow within the respiratory air sac system. The complex breathing system allows birds to fly horizontally in steady level flight.

Various pneumatic and hollow bones such as vertebrae or limb elements have holes in them to accommodate air sacs extending from the lungs. The pneumaticity of bones makes the bird skeleton light, thereby allowing flight. Lightness of structure is especially marked among some larger soaring birds. For example, a magnificent frigatebird, flying on 2-meter wings and weighing only 1.5 kilograms, has a skeleton that makes up just 5% (75 grams) of the total body weight. This is less than the mass of its feathers. Birds have found other ways to lighten the load in addition to hollowing out their bones. For instance, they keep their reproductive organs tiny for most of the year, greatly enlarging them only during the breeding season. To keep their weight low and feathers dry, they forgo the luxury of sweat glands and excrete uric acid instead of urine. Birds have also lost the right ovary, oviduct, and external genitalia to reduce the weight in flight. Most birds do not have a penis. Instead, both male and female birds have a cloaca—a posterior opening for the intestinal, urinary, and reproductive tracts. Musculature is concentrated on the underside of the bird, establishing a steady center of balance around the center of gravity.

Flight necessarily imposes limitations on body weight. As animals get larger their body masses (M) increase approximately with the cube of their lengths, whereas their surface areas increase only with the square. The mass-specific power available from the flight muscles is assumed to scale as $M^{-1/3}$. As available power decreases with increasing body size, the range of attainable flight speeds becomes progressively reduced until the largest birds cannot flap anymore. Scaling plays a role in flight performance. Small fliers have a great deal of power for their weight so they have no problem taking off or landing vertically, which adds to their maneuverability. Modern flying birds are very light for swift flying; the mean weight ranges from 10 grams to 1 kilogram, dwindling sharply above and below these limits (Pennycuick 1986). As birds get bigger, these advantages diminish, to the point that the largest flying animals—albatrosses, vultures, eagles, and condors—depend on soaring rather than powered flapping flight. Beyond a certain size, sustained flight becomes prohibitive because of energy requirements and the physical limitations of bone and muscle. We have empirically estimated that the largest bird capable of soaring would be close to 80 kilograms (fig. 12.5). The great kori bustard of Africa is the largest flying bird, with body mass up to 18 kilograms, but it takes off only with great difficulty, running like a taxiing aircraft to pick up flight speed. Larger birds (10–15 kilograms) like vultures, storks, swans, cranes, bustards, and albatrosses spend most of their time soaring, which extracts energy from the air with very little muscular effort (Pennycuick 1986). The largest known flying bird was *Argentavis magnificens* from the Late Miocene of Argentina (Campbell and Tonni 1983; Chatterjee et al. 2007). It was a vulture-like soaring bird with a wingspan of 7 meters, weighing as much as 70 kilograms. *Argentavis* probably used thermals for soaring over Argentinean pampas (fig. 11.5). At the opposite end of the scale is the tiny bee hummingbird (*Melisuga helenae*) of Cuba, the smallest bird. When fully grown, it measures about 5 centimeters and weighs about 3 grams.

A Streamlined Body

The relationship between the shape of a bird's body and the angle at which it meets the airflow is a complex phenomenon. During forward flight, a bird's body generates drag that tends to slow down its speed. As the bird moves through the air, the air resists its motion and the resistance force, drag, is directed along and opposed to the flight direction. Streamlining the bird's body and wings like a teardrop or a spindle reduces pressure drag, ultimately to insignificance. Imagine a smooth, spindle-shaped rigid object moving through air. Forms with such contours—blunt and rounded in front and tapering to a point in the rear—are typical of the bodies of most birds. When the leading edge of a streamlined form cleaves the air, it forms a thin boundary layer of air flowing over the surface of the object, where successive layers of air

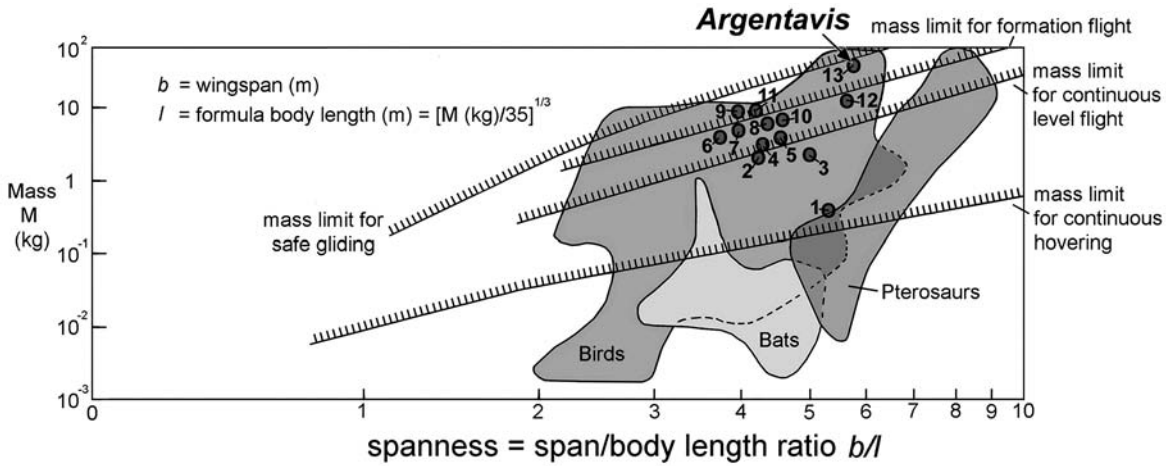


Figure 12.5. Relation between mass and spanness in three groups of vertebrate fliers (birds, bats, and pterosaurs). As size increases the range of flying styles changes. The chart shows four sloping hatched bands, the lower edges of which correspond to the theoretical estimates in the upper mass limits, respectively; note that *Argentavis* occupies the upper size limit of gliding flight (after Chatterjee et al. 2007).

slide past one another smoothly without any eddies or vortices, called laminar flow. During normal flight, birds preserve laminar flow within the boundary layer to minimize drag. When the boundary layer breaks away from the surface, it results in increased drag, or stalling. The spindle-shaped body of a bird with extended wings offers minimum air resistance because it causes the least deviation in the path of the boundary layer, which follows a steady, smooth route. Pressure is highest at the most anterior point of contact between the object and the moving air, and is lowest behind the object. When a bird flies, pressure drag is dramatically reduced in its streamlined body plan with its tapering front and rear ends through millions of years of evolution.

The nature of the body's surface also affects friction drag because a rough surface will generate more skin friction as a result of the air flowing over it than a smooth one. Birds with a smooth feathery coat reduce friction drag considerably. To reduce friction drag further, a bird would have to be free from all projections such as legs. In normal flight, the feet are carried horizontally, beneath the tail or tucked up under the light feathers, with the ankle joints fully flexed to conform to the streamlined body and reduce drag.

The Production of Lift

The wing of a bird is an airfoil of high camber, presenting a curved, streamlined surface that is thicker at the leading edge but gradually thins toward the trailing edge. The distance over the top is greater than the distance across the bottom. When a bird moves through the sky, the air at the front separates as it flows over the wing's surface. Since the top surface of the wing is more curved than the bottom, the upper airstream moves faster than the lower airstream to reach the trailing edge. That is because it must go a longer distance in the same amount of time. The difference in airspeed causes a difference in air pressure. The airfoil design of the wing generates unequal pressures, less above and more below, to produce lift. According to Bernoulli's principle, as the velocity increases in a flowing fluid, the pressure decreases. The airspeed is greater over the upper surface, as indicated by closer streamlines, than the lower surface. As the airflow speeds up in moving the top surface of the wing, the pressure there decreases more than the pressure across the bottom, thus creating an upward force, or suction, on the top of the wing and generating lift. It is the continuing pressure differential over the upper and lower surfaces

that creates and sustains lift. Lift is what keeps a bird up in the air while it is flying.

During lift generation by a pair of wings, a few factors come into play: wing size, airspeed, air density, and angle of attack. The role of wing size is straightforward. A wing's lift (L) is directly proportional to the wing's area (S). So a wing twice as large can carry twice as much weight. The relationship between lift and airspeed involves air density, which is about 1.25 kilograms per cubic meter at sea level. The force generated by the airflow around the wings is proportional to airspeed (V) times air density (d). This means that if a bird flies twice as fast, it generates four times as much lift. The third factor is angle of attack. One way that a bird can increase lifting power is by tilting its wings to increase their curve. In a flapping wing, each section performs a separate task; the inner wing, with secondary feathers, provides lift, while the outer wing, with large primaries, provides thrust (fig. 12.6A). Both lift and thrust depend on the angle of wings with respect to the direction of airflow, the angle of attack. When the wing is angled upward, air deflected from its lower surface provides additional lift. If the angle is too great, turbulence reduces lift and increases drag. Birds change the angle of attack of their wings to fit the circumstances. When the angle of attack is low, the airflow over the wing's airfoil generates the forces of lift and drag. The interaction of these two forces, the lift-to-drag ratio, produces a resultant force that varies with the angle of attack. As the angle of attack rises to about 6°, the lift-to-drag ratio is maximum. Birds use their wings at an angle of attack of 6° during long-distance flight. They generate lift by tilting up the inner wing against the air current to an appropriate angle and can adjust the angle of attack of their wings to suit circumstances (fig. 12.3C–F). If the angle of attack becomes too great (> 15°), the airstream cannot follow the upper surface and the airflow breaks away, resulting in a turbulent wake with less negative pressure and a loss of lift. The angle at which this occurs is called the stalling angle. The alula on the first digit of the wing reduces the chance of stalling. By moving that digit, a bird can separate the feathers of the alula from the rest of the wing, creating a slot that helps channel air over the flight feathers to prevent eddies.

Power, or Thrust

Experiments show that the basic ingredients of flight are power, lift, and control. Without a power source, a bird is unable to fly at a level altitude or to climb. Birds power flight primarily by flight muscles that flap the wings at the shoulder. In flying birds, flight muscles average 20% of the body mass. For example, a 10-kilogram albatross has 2-kilogram flight muscles. In order to fly, birds need increased power to support their bodies in the air, to overcome the air friction against their bodies and wings, to power their wings and tail muscles, and to support their increased circulation and breathing rates while flying. Other than flight muscles, there are additional power-increasing adaptations in the physiology of birds, including warm-bloodedness, heat-conservation feathers, an energy-rich diet, efficient digestion to acquire fuel for metabolism, a four-chambered heart for efficient circulation, and a highly efficient respiratory system with air sacs.

Thrust is a force that overcomes drag. A bird that is flying forward must drive air both downward for lift and backward for thrust. Once lift is achieved, power, or thrust, must be generated for forward motion. This power comes from the flight muscles that can move the wings up and down and back and forth, relative to the glenoid of the shoulder girdle and the longitudinal axis of the body (fig. 12.6B). The wing is constantly changing velocity as it flaps, slowing down and stopping at the ends of the downstroke and upstroke, and then accelerating into the next half stroke. The tips of the wings not only flap up and down but also twist forward on the downstroke to propel the bird forward. Flapping flight entails a downstroke, when the wing moves down and forward to provide thrust, and an upstroke, when the wing moves up and back in medium flight speed (Rayner 1981). With a complete wingbeat cycle, the wings create a lazy figure eight. The primary feathers, attached to the trailing edge of the hand in such a fashion that they push against the air during the downstroke of the wing, propel the

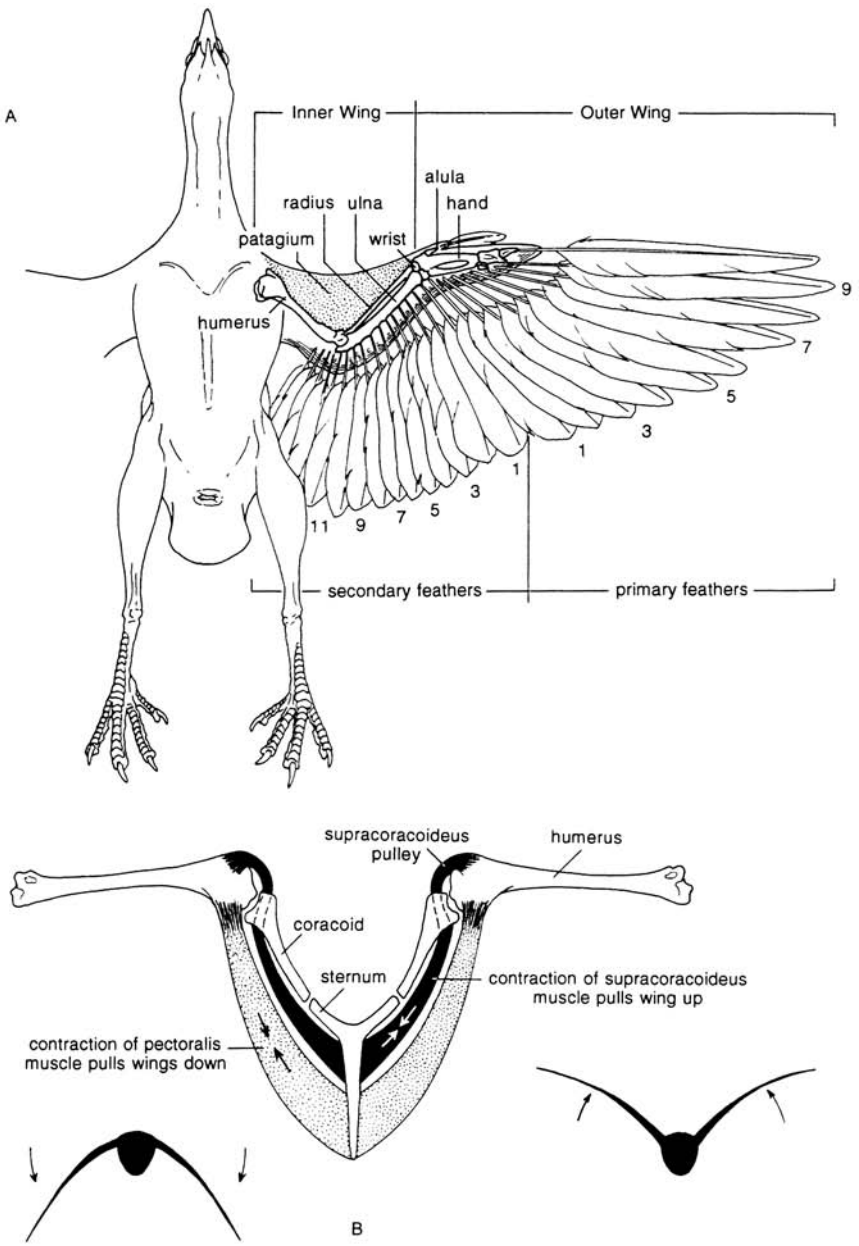


Figure 12.6. Wing structure and flight muscles in birds. A, ventral view of the left wing of the pigeon (*Columba*) showing the inner and outer wings, as well as the number, location, and attachments of major flight feathers. The primary feathers attached to the hand propel the bird forward, whereas the secondary feathers attached to the ulna provide most of the lift. Note the strong asymmetry of the primary feathers; each feather acts as an individual airfoil. B, diagrammatic view of the shoulder girdle bones of a bird showing how the flight muscles operate during flapping. The flight muscles are anchored to the keel of the sternum and pull the humeri of the wings up and down (after Chatterjee 1997).

animal forward (figs. 12.3E, 12.6B); this, in turn, creates vortex wakes that are forced backward as the bird moves (Rayner 1988). The twisting of the wing toward the tip to reduce the angle of attack is the most important element in the downstroke. The upstroke serves to position the wing for the subsequent downstroke. The outer wing is more flexible than the inner wing and does most of the propelling at the tips of the primary feathers. While the inner wings tilt up to provide lift, the outer wings tilt down so that their airfoils create forward rather than upward thrust (fig. 12.6B). As the inner wings descend, their thrust pulls them forward, and they in turn pull the outer wings. Birds maneuver in flight by controlling the patterns of lift and thrust.

A Control System

The ease with which birds negotiate confined, obstacle-cluttered airspace clearly indicates their superb control systems. Birds fly using a delicate controlled interaction with surrounding airflow. They routinely execute aerial maneuvers that are far beyond the capabilities of most modern aircraft without mishaps. They can change course, slow down, or accelerate in the very last moment with superb control. The complexity and variabilities of the aerodynamics during these maneuvers are formidable, and are aided by fine neural control. They need the transmission of information from the body to the brain about the continual adjustment of the wings in response to airflow over them.

Birds, like modern aircraft, have developed a wide variety of control surfaces on their wings and tail for steering and maintaining their balance during flight by morphing wings. During aerial turns, ailerons, the movable surfaces on aircraft wing trailing edges near the tips, are deflected in opposite directions for roll and control. Large deflections are needed only to initiate or make quick changes in turns. In birds, differential twisting or washout in both wingtips function like ailerons. The alula, or bastard wing, of birds corresponds to slats on the wings of an aircraft, which can be manipulated during slow speed or landing. The alula allows the wings to achieve a higher than normal angle of attack—and thus lift—without resulting in stalling. Birds can control wingspan, especially during the upstroke, by folding their wings. Similarly, in concert with the tail birds can change the camber of the wings for different speeds or change the direction of flight like a rudder. Feathers act like mechanoreceptors to sense the direction of the wings. Wing morphing and sensorimotor architecture make birds more agile and maneuverable than aircraft.

Flight requires fine coordination between muscles and senses to main stability. The central nervous system of a bird consists of the brain, the sense organs, the spinal cord, and the nerves. Nerves carry messages from the eyes or ears to the brain. During flight, the bird's sensory apparatus assesses the environment and conveys impressions through electric pulses, which stream to the spinal cord for immediate reaction or are transferred to the brain for central processing. The forebrain is considerably enlarged in birds for processing sound, touch, and sight, and to adjust behavior to new situations.

Birds possess certain remarkable sensibilities in relation to intricate flight. They live in a world that is dominated by sight and sound. Their sense of vision is so highly developed that for most birds, three of the four senses—touch, smell, and taste—are irrelevant. Birds are highly visual animals and use several sensory cues during flight. They have enormously large eyes that provide keen sight, sharp images, and superb color perception. Most birds have flat eyeballs with large retinas, which are excellent for scanning the landscape. A bird can gain more information about its surroundings through its eyes than through all its other sense organs combined. High vision acuity on the fovea of a bird's eye provides a vision-dominated sensing system that allows precise distance judgment to avoid collisions. In the brain, the optic lobes are large, correlating with the visual acuity of birds.

Birds have a relatively large cerebellum, or hindbrain, which plays important roles in balance, coordination, and proprioception, the positional equilibrium. The inner ear is located on the side of the cerebellum, which is the sensory receptor for equilibrium and sound. Next to vision, the sense of hearing and equilibrium is also well developed in birds. Birds are able to hear sounds

of frequencies much higher than those humans can perceive. This ability helps them locate burrowing insects and other prey that emit high-frequency sounds. Some night birds such as owls have excellent hearing. Because of their hearing acuity, birds use their calls and songs eloquently to communicate to potential mates, rivals, and predators. Song allows birds to speak better than any other family of creatures. The vocal skills of birds derive from the unusual structure of their sound-producing equipment, the syrinx at the bottom end of the windpipe.

The inner ear of birds, in addition to sensing sound, contains gravity and rotation sensors in the form of semicircular canals. The vestibular apparatus containing three semicircular canals, which are oriented roughly in the three planes of space, functions as a well-developed equilibrium-sensing system like a gyroscope during flight. The large vestibular organs in birds provide body information that, perhaps with wing muscle load sensing and probably with input from vision motion sensing, allow for stable controlled flight. The enormous flocculus at the center of the canalicular system has important neural integration with the vestibular system, the eye muscles, and the neck muscles for stabilizing gaze. Birds have a remarkable capacity to steady their heads as their bodies undergo dramatic oscillations during flight. Since the eyes are fixed to the head, gaze stabilization and control is effected by control of the head in relation to body posture with the neck muscles. The stable cockpit of the head provides sophisticated sensory mechanisms for flight control with a complex feedback system from the wings.

Short neural circuits of the spinal cord mostly control wing and leg movement; they carry neural messages to the brain stem, the cerebellum. The spinal cord assesses, reacts, and conveys sensory information to and from major nerves and the brain. The brain sends signals to the nerves, which operate muscles. The precise neuromuscular coordination of wings allows birds to perform intricate flight. Birds have neuronally innervated skeletal musculature. In free flight a bird's powerful pectoral muscles provide the downstroke and supracoracoideus muscles produce the upstroke. Other forelimb muscles are used for extension, rotation, and retraction of the wings in all phases of wing stroke.

Maynard-Smith (1952) argued that early birds such as *Archaeopteryx* retained a long bony tail for stability. Later birds such as Pygostylia lost this bony tail to become unstable but more maneuverable; their nervous systems acquired sophistication and reflexes needed to do more and more acrobatic skills. They used their flexible wings to turn, increase or decrease speed, and change the direction of flight. Increasing maneuverability means decreasing stability.

Like other animals, birds feel with sensitive receptors that are attached to the nerves. These receptors are scattered all over the body. Birds can sense the speed and direction of the airflow over their wings with the help of feather follicles that act like mechanoreceptors, which are pressure-sensitive sensors. The stimulus from the feather sends information about the airflow around that region of the body to the brain for processing and adjusting wings for flight orientation and stability. In addition to airflow sensors in the wings, many birds have magnetic sensors, built-in-compasses, probably situated in the eyes that are useful for long-distance migration. Vision and mechanosensing are apparently used at all levels in birds as a sensory response flight control system that is characterized by intricate sensory interconnection and feedback.

Flight Dynamics

When an aircraft is flying horizontally, its weight is balanced by the average lift of the wings, and the drag on the wings and body is balanced by the forward thrust. In a shallow glide in still air, there is no propulsive thrust, but there is a component of gravity acting forward along the sloping path. Unlike airplanes, flying vertebrates get both lift and thrust from their wings, and many are capable of hovering flight at zero airspeed. In this respect, birds are like helicopters, which depend on their rotors for both support and thrust.

Most functional analyses of flight performances of flying animals have centered on birds, taking advantage of classical aerodynamic equations used in aircraft design. The most common method for approximate performance estimation is an aircraft-like model (Prandtl and Tietjans 1934), which uses familiar parameters such as lift and

drag coefficients, wing area, wing aspect ratio, and span efficiency (Pennycuick 2008). In this method, the power required to maintain steady level flight is calculated as the product of aerodynamic drag and flight airspeed. The total drag is calculated as the sum of two components: induced drag, which is the penalty that must be paid for the production of aerodynamic lift, and a component (sometimes called zero-lift drag) assumed independent of lift, comprising pressure drag and surface skin friction. This simple method has limitations: it predicts infinite induced drag and power at zero airspeed and therefore cannot be used without modification for performance estimation in hovering or near-hovering flight. Pennycuick (2008) developed a computer model, the Flight program, based on classical aerodynamics, which calculates the rate at which a flying animal requires energy for whatever it is doing.

A second model, known as momentum stream tube theory, was originally proposed for straight wings by Ludwig Prandtl (Prandtl and Tietjans 1934), developed farther by helicopter designers (Stepniewski and Keys 1984), and adapted to animal flight (Templin 2000; Chatterjee and Templin 2004a, 2004b, 2007, Chatterjee et al. 2007). It avoids the zero-speed problem by assuming that a cylindrical tube of air having a cross-section area (A) with diameter approximately equal to wingspan (b), or rotor diameter, initially approaching the wing or rotor at flight speed (V), is deflected downward through an angle (θ), which may vary from 90° in hovering at zero speed to a small angle in cruising and high-speed flight. The flight power is equated to the change in kinetic flow in the streamtube from far upstream to far downstream, which is required to balance lift and aerodynamic drag. Surprisingly, two methods, the aircraft model and the streamtube model, produce essentially identical results in gliding and flapping flight at speeds that are usually above 5–10 meters/second.

Flight performance depends on the Reynolds number, a dimensionless number that gives a measure of the ratio of two opposing forces, inertial forces and viscous forces, in the airflow when the bird is flying. Inertia is a property of an object that allows it to remain at a constant velocity unless an outside force acts on it. An object with large inertia will strongly resist a change in velocity, whereas an object with small inertia will almost instantaneously start or stop when acted on by some external or internally generated force. Viscosity, on the other hand, is the resistance of a fluid to flow under the influence of an applied external force. It is the source of drag on objects moving through the fluid. For such an object, inertia strives to keep the object going, whereas viscosity tries to stop it. The Reynolds number determines whether viscous drag or pressure drag is dominant. For most flying birds, pressure drag is more important than viscous drag. Small creatures move slowly and have low Reynolds numbers, while big animals move fast and have high Reynolds numbers. Bird wings operate over a low Reynolds number range of about $1\text{–}5 \times 10^4$, which is relatively low for an aircraft. Low Reynolds number aerodynamics is important to a number of flying animals such as insects, birds, bats, and pterosaurs as well as small, unmanned air vehicles such as micro air vehicles (MAVs). Because these fliers are lightweight and operate at low speeds and low Reynolds numbers ($< 10^5$), they are sensitive to wind gusts.

To analyze the flight performances of feathered dinosaurs and birds, we have used two computer algorithms, ANFLTPWR (animal flight power) and ANFLTSIM (animal flight simulation), which are based on a streamtube model using several flight parameters, such as body length, mass, weight, wing area, wingspan, aspect ratio, wing loading, root chord-to-body length ratio, power available, power required, and cruising speed (Templin 2000).

Unpowered Flight: Gliding and Soaring

Gliding and flapping flight are the basic types of avian flight. Flapping flight is arduous, which is why many species of birds have discovered how to stay airborne without flapping their wings. Gliding is a simpler and cheaper way of flying than flapping wings. It is energetically economical and a relatively fast mode of travel. The wings still provide lift while gliding, but without flapping there is no thrust and the bird will gradually sink to the ground. Thrust can be produced by gravity force while the animal is descending. Large birds fly by gliding and soaring—harnessing the power of the wind or the Sun to keep them

in the air. In these birds, the gliding ratios are high, and gliding therefore gives them as overall advantage over smaller birds with relatively poor glide ratios. Moreover, larger birds have problems carrying sufficient fuel and musculature to meet the energy demands of continuous flapping flight, and use gliding as a means of reducing their overall energy cost.

The trick of gliding is to make use of speed and altitude either previously gained by wingbeats or available from wind currents. Gliders stretch their motionless wings to form one lifting surface and passively descend through the air by the help of gravity without any flapping. They can glide a great distance without any muscular effort. The combined result of two forces, the downward pull of gravity and upward and forward lift, move the glider ahead. The forward component of the thrust is sufficient to overcome drag on the body.

Several factors determine how well a bird can glide. The first is the efficiency of its wings in flight, the ratio between lift and drag. The gliding angle directly controls the lift-to-drag ratio. The higher the lift-to-drag ratio the glider has, the better it will glide. For example, a sparrow with a wingspan of 20 centimeters has a lift-to-drag ratio of 4 because it flies at a low Reynolds number, whereas in an albatross the value is 19 because a large albatross with a wingspan of more than 3 meters flies at a high Reynolds number. The larger the wing area, the better the glider. The ability of a wing to produce lift is proportional to its surface area. A wing twice as large can carry twice as much weight. The best gliders are birds with large wing areas that provide high lift-to-drag ratios. Eagles and vultures are all good gliders over land with large slotted wings. Seabirds like gulls, frigatebirds, and albatrosses have long and narrow wings for gliding and soaring over oceans.

Another important factor is how much weight the bird's wings must carry. The amount of wing area a bird has, compared to its weight, is called its wing loading (body weight divided by wing area). A glider with a lower wing loading flies slower but needs to use less of its lift to overcome its weight, so it can move forward in a longer, flatter glide.

Another way of measuring a bird's gliding ability is by noting its sinking speed, or the amount of height it loses in a given time. Sinking speed is determined primarily by wing loading, so that lighter, larger gliders descend more slowly than do smaller, heavier ones. A glider sinks rapidly if it glides slowly or fast, but at intermediate speed it loses height less quickly and can stay airborne longer.

Gliding is a passive mechanism of flight where height is continuously lost with an angle of descent of less than 45°. Good gliders cover long distances with little descent. However, when the rate at which upward wind current lifts a glider is equal to or greater than its sinking speed, it can stay aloft indefinitely. Some birds may glide between flapping to take a brief rest or because their desired path is downward.

Colin Pennycuick (1968) built a wind tunnel to study the gliding performances of birds. If the wind tunnel was tilted up at a sufficiently large angle, the bird did not need to flap its wings, but could simply glide into the wind. By varying the speed of the jet and the angle of tilt, Pennycuick calculated the gliding performance at each speed as a polar curve, which is a plot of horizontal speed versus sinking speed. Sinking speed is determined primarily by wing loading, so that lighter, larger gliders descend more slowly than do smaller, heavier ones. Sinking speed is equal to the ratio between the power (P) needed to maintain horizontal flight and the weight (W), and is called power loading. In a glide polar curve, the sharp downturn of the left side of the polar curve indicates the minimum airspeed at which a glider can fly, or its stall speed. The point of minimum sinking speed is at the top of the curve, where the flier can glide for the longest duration from a given altitude. The third point represents the airspeed at the best gliding ratio. At this point, a bird can glide the longest distance from a given altitude. The speed for the best gliding angle (maximum lift-to-drag ratio) can be found by drawing a tangent between the glide polar and the origin. Flying animals usually glide at speeds faster than the minimum sinking speed to avoid stalling. When a glider glides slowly, it loses height quickly because induced drag is high. Similarly, when it glides fast, it also loses height quickly because profile drag is high.

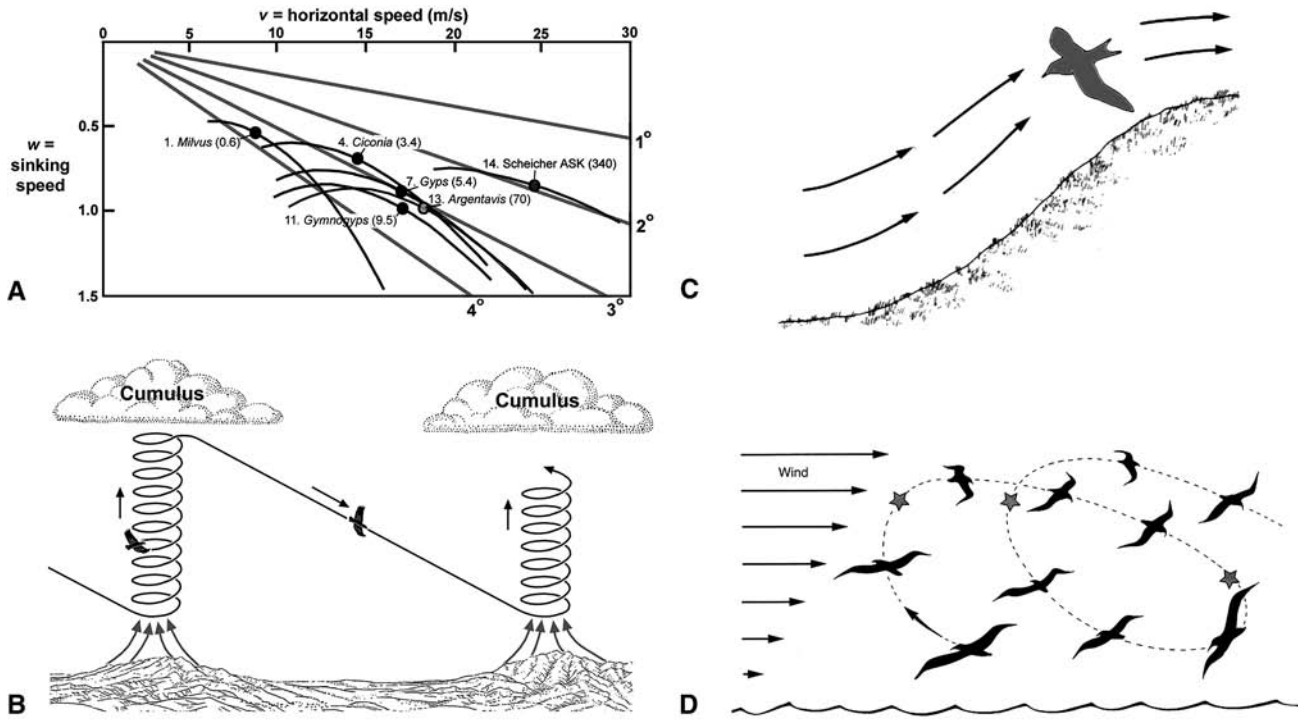


Figure 12.7. Gliding and soaring techniques of birds. A, a generalized glide polar curve for soaring birds, where sinking speed (*w*) is plotted against horizontal speed (*v*). The slight downturn on the left side of a glide polar indicates a stall. The high point on the polar on the right side of each is the minimum sinking speed (i.e., the speed at which the flier can glide for the longest duration from a given altitude). A glider sinks rapidly in still air if it is traveling slowly or fast, but sinks less rapidly at intermediate speeds. We used the ANFLTSIM computer program to calculate the values of horizontal speed against the sinking speed to generate the glide polar curve. Flying animals normally glide at speeds faster than the minimum sinking speed to avoid stalling. The speed for the best gliding angle (maximum lift-to-drag ratio) can be found by drawing a tangent between the glide polar and the origin. The glide polar for the Miocene bird *Argentavis* (the largest flying bird) is compared with four species of extant soaring raptors: black kite (*Milvus migrans*), white stork (*Ciconia ciconia*), white-backed vulture (*Gyps africanus*), and California condor (*Gymnogyps californianus*), as well as the motor glider Scheicher ASK (340). Lines of glide slope angles are shown. For most birds, including Argentavis, the minimum glide slope is close to 3°, indicating excellent gliding capability (after Chatterjee et al. 2007). B, soaring in thermals; many landbirds soar by circling in thermals that require climbing successive thermals and gliding in the desired direction during cross-country flight, C, slope soaring, which takes advantage of ascending air on the upwind side of a hill. D, dynamic soaring in a wind whose horizontal speed increases with altitude. The bird alternately ascends and descends using the wind gradient above the sea for soaring, extracting energy from the gradient. By zigzagging across the wind, a bird can fly long distances with minimum effort (after Chatterjee et al. 2007).

We used an ANFLTSIM program to calculate these values for a wide range of gliding birds that suggest that gliding performance increases with increasing body mass (Chatterjee et al. 2007) (fig.12.7A). Gliding performance of birds is calculated as a lift-to-drag (L/D) ratio, called the glide ratio or finesse (*F*).

While gliding animals descend to have gravity-powered flight, many birds can ascend without flapping their wings. Soaring flight is staying aloft by gliding at an altitude where height is maintained or gained by rising air. Soaring birds take advantage of updrafts from wind currents to lift them into the air. Vultures, albatrosses, eagles, storks, and many hawks are masters of soaring. In soaring, a bird obtains energy from the upward currents of air in which it flies. The only way a gliding or soaring bird can maintain or gain altitude is to find updrafts that exceed the rate at which it is sinking. Speed is maintained by extracting energy from the wind. Soaring flight is considerably cheaper than flapping flight. Many large birds use soaring when searching for food or during migration.

Birds take advantage of updrafts from wind currents to use two types of static soaring while holding their wings still: slope soaring and thermal soaring. In slope soaring, a bird flies in a region of rising air caused by upward deflection of wind over a ridge or a cliff. If the sinking speed of the animal is less than the velocity of the rising air, the bird is able to remain airborne indefinitely without flapping its wings. As long as the upward velocity of the rising air over the mountain slope is greater than 1 meter/second, which is fairly common, a bird can exploit slope soaring for a long time. For example, a moderate wind blowing at 20 kilometers/hour directly along a 10° slope will have an upward velocity of 1 meter/second. Slender, pointed wings enable gulls to glide on updrafts by cliffs and hillsides. Some birds can attain speeds of 60 to 70 kilometers/hour by soaring along the ridge of a mountain where wind blows constantly.

Birds also exploit thermals, or rising columns of warm air, over open areas of plains during foraging. Large broad-winged landbirds, such as eagles, buzzards, storks, and vultures with slotted wings, are masters of thermals and travel cross-country by gliding in circles where altitude is maintained or gained by rising air (Pennycuick 1973). They soar effortlessly for hours and often climb 2 to 3 kilometers into the air within a thermal in subtropical and tropical regions. Thermal soaring does not depend on wind, but on convection currents created by solar radiation that heats the ground to well above air temperature. Thermals are produced when the sun heats the ground unevenly. For example, a large, exposed rock surface will warm up more rapidly than the surrounding vegetation (fig. 12.7B). As a result, air above the rock surface is warmed differentially and begins to rise as a column like an invisible elevator. Thermals can be continuous chimneys of rising air, or a series of discrete, doughnut-shaped bubbles. A thermal contains a zone of rising air about 1 to 2 kilometers in diameter with vertical velocity strongest in the middle and decreasing outward. Soaring birds use such landmarks to find thermals. Another signpost is a canopy of cumulus clouds over one or more thermals, which are visible from long distances. Once a bird locates a thermal, it senses the lift and spirals around to take advantage of it; other birds then converge on it. Vultures and eagles use the same technique. Once within a thermal, a bird can circle and climb vertically within the rising column as long as the upward speed of the thermal is greater than the sinking speed of the bird. As it reaches the top of the thermal, the bird can glide straight to an adjoining thermal and gain height again by riding the rising air. Many birds can fly all day just by riding thermals and travel cross-country at a speed of 40–50 kilometers/hour. Vultures over the Serengeti Plain in East Africa can make a round trip of 200 kilometers by skillfully riding upward while searching for carrion. To stay within a thermal, a bird must be capable of turning fairly tight circles as close as possible around the center. When circling, the bird banks such that its wing lift has a force component directed to the center of the turn to balance the centrifugal force.

The wings of seabirds that soar over oceans are much narrower than those of land soarers. Thermals form over the oceans along the equatorial belt at the interface of cold air over warm water. During summer in the tropics, the trade winds bring in cool air over warm water, whereas during winter at high latitudes cool air from the polar regions flows over relatively warm sea. Such thermals remain active at night because the sea remains warm while land cools (Burton 1990). Many seabirds such as herring gulls and frigatebirds ride on thermals over vast open oceans along the equator for hundreds of kilometers, exploiting the updraft to boost their soaring performance.

A third type of soaring is dynamic soaring without updrafts. Many seabirds such as albatrosses and frigatebirds exploit changes in wind speed with height over the open oceans with strong, continuous unidirectional winds. Steady, prevailing winds blow horizontally across great stretches of the ocean like a deck of cards, and albatrosses follow these wind patterns in their travels. The air is quite still near the surface of the sea even when the wind is blowing strongly just few meters above because the friction is greatest near the water surface. The higher the altitude, the faster the wind blows (fig. 12.7C). The albatross exploits this gradient of horizontal wind speed to soar. It can rise to gain height like a kite in a breeze,

and then glide down in any direction. By repeating this maneuver it can fly thousands of kilometers without flapping its wings, and by tacking it can travel anywhere, regardless of wind direction. Over the sea, lift coefficients average 0.9–1.0. The albatross starts out on a steep downward glide from a height of about 20 meters to gain speed, momentum, and kinetic energy with a tailwind. As it loses altitude, it gains groundspeed. At the bottom of the downward glide, just above sea level, the albatross turns around and climbs back steeply into the wind, at first using momentum gained in a downward glide. As it climbs higher and higher, the bird loses momentum as the wind layers move faster and faster, aiding its lift. Once having regained altitude, it turns into another downward glide to avoid stalling. Repeating these upward and downward movements in a zigzag course, an albatross can stay aloft for hours and even days without flapping its wings. Soaring may be the most economical method of long-distance locomotion (fig. 12.7D).

Powered Flight: Hovering and Flapping

Powered flight requires much more energy than gliding. Energy comes from the flight muscles that move the wings up and down to keep the animal aloft. In powered flight, most flying is done by active beats of the wings. The wingbeat in flapping flight is complex and varies considerably in geometry according to flight speed and to the design of wings. Most birds depend almost entirely on powered flight, propelling themselves by flapping their wings. Flapping flight is much more complicated than flight with fixed wings because of wing forming and the resulting unsteady fluid dynamics. The continuous available power for flapping flight has been estimated from many measurements of metabolic rates for birds.

Pennycuick (1972) suggested a simple allometric equation for conversion of metabolic energy to mechanical power:

$P_{available}$ (total metabolic power available for a bird in watts) = $10 \times$ body mass (in kilograms)$^{0.66}$

Using this equation, we can calculate the power available for a 2-kilogram bird as 16 watts.

Many small birds, such as hummingbirds, beat their wings nonstop up to one hundred times per second to hover while sipping nectar. Hovering is the most expensive form of flying. Flying to stay in one place, while supporting body weight, is a difficult feat. Birds hover by beating their wings in a near-horizontal plane, with their bodies tilted at a steep angle to drive air vertically downward, similar to insect flight. A kestrel can hover for longer periods than a hummingbird by using a headwind as its keen eyes pinpoint small animals on the ground. The wings beat rapidly in a forward motion and the tail is fanned out as a brake. Most birds hover while facing into the wind. The wind blows them backward at the same rate that they are moving forward, so that they stay still. In hovering flight, the main wing movement is centered at the shoulder joint, while the entire wing remains stiff.

For many birds, being able to pursue prey or escape enemies over short distances by flapping flight is much more important than being able to stay in the air by gliding for a long time. Flappers, like the peregrine, have large hand sections compared to their small inner wings. A broad rounded or tapered wing is best for this type of flight because it gives good acceleration and can be adjusted by steering. In powered flight, flapping wings provide both lift to keep the bird airborne and horizontal thrust to move it forward; lift is achieved by the airfoil action of the wings, and thrust by flapping the wings up and down in a complex manner. In a flapping wing, however, each section performs a separate function. The outer wing is mainly responsible for flapping strokes. It involves a downward and forward power stroke with the wing fully extended to provide thrust, followed by an upward and backward stroke with the wing partially retracted (Rayner 1988). With a complete wingbeat cycle, the wing creates a lazy figure eight. The tips of the wings not only flap up and down but also twist forward and downward to propel the bird forward. The greater parts of aerodynamic forces are generated during the downstroke, for in this phase lift points forward, providing both weight support and thrust. The upstroke is largely a recovery stroke but it can generate considerable lift in some circumstances with wake vortices. It serves to posi-

tion the wing for the subsequent downstroke. The inner wing provides lift to overcome gravity, while the outer wing generates thrust. Lift is achieved by the airfoil action of the wing, and thrust by twisting the tips of the wings. While flapping, birds systematically twist their wings to produce aerodynamic effects in ways that the ailerons of an aircraft operate. With different degrees of twisting between wings, a bird is able to roll.

Vance Tucker (1968) pioneered in studying the flapping performance of birds in wind tunnel experiments where he measured the metabolic rate in flight. Flight power is the rate at which bird consumes metabolic energy and generates mechanical work as it flies. Tucker trained a budgerigar to fly in a specially built wind tunnel and calculated how much energy the bird used at various airspeeds. He calculated the aerodynamic power (*P*) required to fly in the wind tunnel at various speeds (*V*) and plotted *P* against *V*. He found metabolic energy costs ranging from 50 watts/kilogram to 120 watts/kilogram for various birds. These U-shaped curves are standard power curves for estimating flight performance, plotted against speed. He found that in horizontal flight, the most economical condition is at the middle of the speed range. It takes more power when a bird flies slowly or fast (fig. 12.8). Using the ANFLTPWR program, we generated the power curves of early birds, where the U-shaped curve is the power required for steady level flight and the horizontal line is the estimated maximum steady power available.

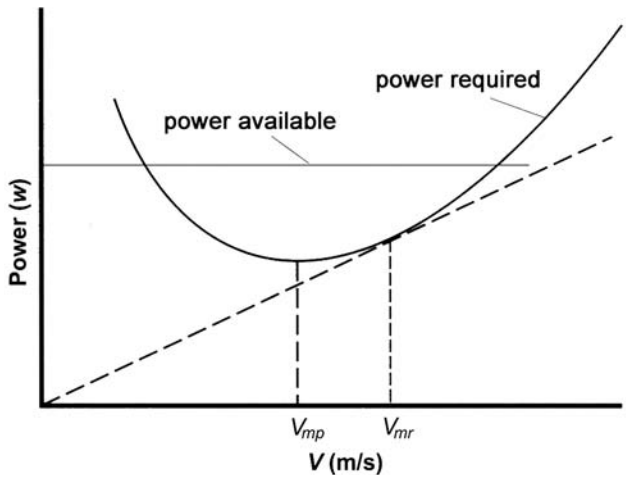


Figure 12.8. The U-shaped power curve for flapping flight. The flight power (*P*) in watts is plotted against airspeed (*V*) in meter/second to generate the U-shaped power curve that gives the metabolic power necessary to fly. Power required for flight is less at moderate speeds (trough of U), the minimum power speed (V_{mp}), and greater at hovering (*left*) and high (*right*) speeds. The left-arm of the U-shaped curve is mainly the penalty that must be paid for the production of lift. The trough of the curve represents the minimum power speed where the bird could fly for the least energy expenditure. A tangent line from the trough shows best cruising speed, the maximum-range speed (V_{mr}). The computer program ANFLTPWR is used for computation of the power required for steady level flight at specified speeds. It also gives the continuous power available (P_{avail}), represented by the U-shaped power curve. The horizontal line represents the maximum continuous power available.

Some large birds, such as geese, ducks, and pelicans, use another strategy to reduce the energy cost of flight during long-distance migration, adopting a very specific V formation in flight that improves aerodynamic efficiency to reduce flight power demand. Following a leader makes it easier for a flock of birds during annual migration. While the leader "breaks a trail" through the air, each following bird gains lift from an updraft off the wing of the bird ahead. Birds can eliminate wingtip vortices by flying in groups. In this mode, each animal follows the leader with the wingtip slightly overlapping the opposite wingtip of the animal ahead and trailing behind, so the formation is V-shaped or a single echelon line. All except the leading animal receive the same benefit from the upwash outboard of the trailing vortex from the animal ahead. If a bird moves ahead of the V-shaped line it finds more power is required to keep up with the flock so that, at the same power, its speed falls until it is back in line. Birds take turns as leader, so the labor is evenly distributed among the flock of birds.

Takeoff and Landing

The most crucial maneuvers in bird flight seem to be takeoff and landing. Takeoff from the ground requires more energy than steady level flight because the bird must accelerate and climb and because takeoff speed is near the left-hand end of the U-shaped power curve (fig. 12.8). Takeoff from the ground is hard work that often requires a short burst of anaerobic power. For this reason, most birds prefer to take off from an elevated perch to secure the needed lift. They simply jump into the air

and spread their wings; the force of gravity supplies the necessary speed to achieve lift for flight. When birds take off from a perch, they do not seem to use excess power; they lose height at first and then swoop up with a large amplitude of undulation.

Small birds (≤ 100 grams) can take off vertically with elegance simply by pushing their legs toward the ground and flapping their wings. Large birds cannot move straight upward so rapidly over a short distance. Whenever a bird with mass greater than 100 grams takes off from the ground, it needs speed to become airborne. The bird must beat its wings more vigorously to obtain the lift it needs along with running. Takeoff and landing are possible for large birds when a long runway is available. The great kori bustard is the largest modern flying bird with a body mass up to 18 kilograms, but it takes off only with great difficulty by running like a taxiing aircraft. Seabirds such as albatrosses, with their long, high-aspect ratio wings, are awkward during takeoff. They can take off only with a long run on a gentle downslope and a light headwind that add a significant increase in forward thrust and power. For this reason, most birds prefer to take off from an elevated perch to secure the needed lift. A cliff-dwelling bird, or one on a tree, merely has to jump into the air and spread its wings; the force of gravity supplies the necessary speed to achieve lift for flight.

Landing, like takeoff, is an arduous task. All birds land as slowly as possible to keep from injuring themselves. They land into the wind to decrease groundspeed while maintaining enough airspeed for lift. The safe landing speed is about 5 meters/second for animals of any size (Templin 2000). Small birds slow down below their minimum cruising speed by tilting up their wings to increase drag and land safely without difficulty. Braking is accomplished not only by raising the angle of attack, but also by tilting the entire body upright, by spreading the tail feathers, and by lowering the legs. Just before touchdown, birds extend their legs forward to absorb the impact of landing. During landing, a headwind helps a bird slow down, shortening the landing run considerably. Landings on water ease the landing shock for small birds, but water takeoffs for very large birds are often awkward and cumbersome. They have a hard time pushing themselves into the air from the surface of the water and prefer to take off from dry land.

The Origin of Flight: How Dinosaurs Became Birds

Evolution of powered flight in birds is generally regarded as a key adaptive breakthrough that helped them to invade a new aerial niche not available to the rest of the dinosaurs. Yet how this remarkable feat came about is still shrouded in mystery. The origin of flight aroused passionate debate among scientists soon after the discovery of *Archaeopteryx*. *Archaeopteryx* provided the earliest unambiguous example of asymmetric flight feathers with its fully developed wings similar to those of modern birds. For this reason, the origin of powered flight is often equated with the origin of *Archaeopteryx* (Ostrom 1976a). The early avialans such as *Archaeopteryx* and *Jeholornis* provided starting points for speculation about how avialans acquired the ability to fly. Understanding the evolutionary steps in the origin of avian flight required the identification of protobirds, the putative ancestors of avialans. The wide acceptance of the theropod origin of birds simplifies the identification of protobirds among theropods such as coelurosaurs. Furthermore, the Jehol feathered coelurosaurs shed critical information about transitional stages of avian flight. As a result, the origin of avian flight is no longer a mystery, but is supported by a large body of fossil evidence.

Two competing models explaining this locomotory transition have been proposed for the origin of flight: ground-up versus trees-down. The cursorial (ground-up) theory maintains that flight evolved in running bipeds through a series of short jumps. As these jumps became extended, the wings were used for balance and propulsion, and the animals began to fly without a gliding intermediate. The arboreal (trees-down) theory states that flight originated in tree-living animals that leaped from branch to branch or from tree to tree, steadying themselves with outstretched wings; they began to glide and then fly from heights to become airborne.

The controversy over the origin of flight remained at a stalemate for several decades. However, two factors rekindled the debate in recent times: the theropod

hypothesis regarding the origin of birds and the newly discovered transitional fossils of protobirds documenting different stages in early experiments in flight. Recent discovery of a series of hundreds of small, exquisitely preserved feathered coelurosaurs and early birds in the Early Cretaceous Jehol Group in northeast China provided the crucial steps of flight evolution from nonflying theropods to flying birds. These feathered coelurosaurs show various transitional stages—from wingless, tree-dwelling, downy theropods to novice parachuters with little wings, to biplane gliders, to monoplane gliders, to large-winged, active fliers, and finally to long-distance maneuverable acrobats. The skeletal evidence for arboreal adaptations of these feathered coelurosaurs together with abundance of plant remains is consistent with them being dwellers in the forest environments of the Jehol biota. The full continuum of aerial behaviors of these coelurosaurs in the context to arboreality may settle the century-old argument whether avian flight began in the trees (trees-down theory) or on the ground (ground-up theory).

Amid these two opposing views, Kenneth Dial of the University of Montana proposed another version of flight origin, called the wing-assisted incline running (WAIR) model (Dial 2003), which is transitional between the ground-up and trees-down theories. In the WAIR model, protobirds are viewed as beginning to climb inclined surfaces by flapping their wings and eventually taking to the skies. The pros and cons of these three major conflicting theories are discussed below in a phylogenetic framework of theropods using biomechanical and fossil evidence. Each theory relies on speculation regarding the paleoecology and functional adaptation of basal avialans and their protobird progenitors.

The Cursorial Theory

Samuel Williston briefly outlined the first cursorial theory in 1879. He suggested that flight evolved through a series of steps: running, leaping, jumping, and flying. This is how the forelimbs of theropods might have transformed into wings. Surprisingly, he gave no other details to support his theory. In 1907 and 1923, the Hungarian paleontologist Franz von Nopsca elaborated on Williston's idea by suggesting that wings would help to increase the speed of an animal as it ran along the ground. He concluded that birds evolved directly from terrestrial cursorial theropods without any gliding stage, and that bipedality preceded the development of flight. However, Nopsca acknowledged that *Archaeopteryx* had already achieved some level of arboreal capacity. Nopsca's ideas on the origin of flight were severely criticized by other workers because the use of wings to increase running speed has no living analogues and because outstretched wings would increase drag and retard takeoff speed (Heilmann 1926; Bock 1986). As soon as the animal left the ground, its legs could no longer propel it forward in the air and it would immediately fall back down.

John Ostrom (1974, 1979, 1985a, 1986) revived the cursorial theory with new vigor as he formalized the theropod origin of birds. Ostrom believed that the hindlimbs and bony claws of *Archaeopteryx* represent the lifestyle of a typical cursorial terrestrial biped and are very similar to those of dromaeosaurs such as *Deinonychus*. He argued that the bipedalism of *Archaeopteryx* would allow free movement of the forearms, making them available for catching insects. In this view, wings evolved from arms used to capture insects; feathers were first present as insulators and later became elongated flyswatters. The feathers would enlarge through time, making them better tools for batting insects. In fact, the entire forelimb would become a large, lightweight insect net. These protobirds would catch insects by chasing and swatting them with their wings. Eventually, as the forelimb evolved into a better tool for catching insects, the motion would turn from swatting into actual flapping flight (fig. 12.9A).

Ostrom's "insect net" theory was heavily criticized on several grounds. His model has four major problems that are difficult to explain (Feduccia 1980, 1995b, 1996; Martin 1983b; Caple et al. 1983; Bock 1983): (1) The motion used to catch insects is very different from the motion used in a flight stroke. Therefore, it is unlikely that such an insect net would evolve into a structure used in active flight. (2) *Archaeopteryx* would damage its wings and feathers for flight if it used them to bat down prey. (3) To catch an in-

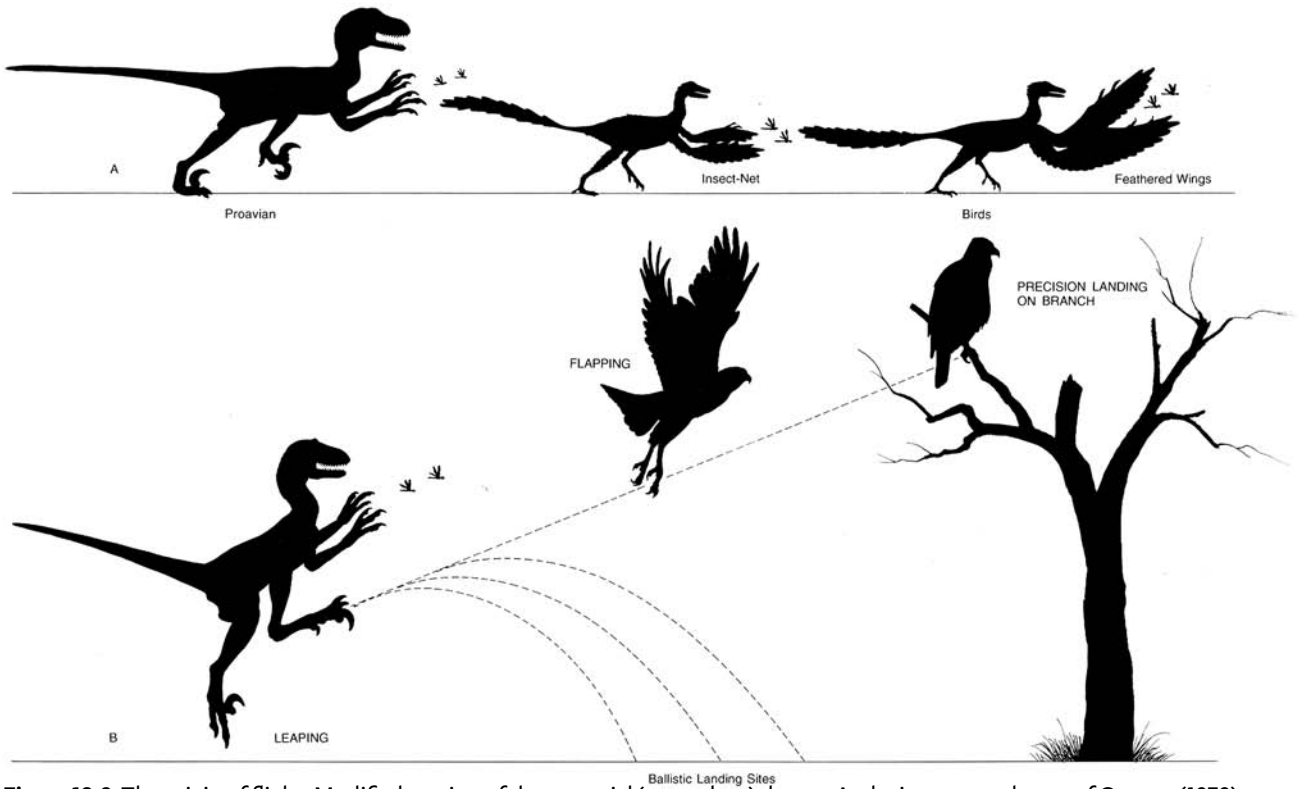


Figure 12.9. The origin of flight. Modified version of the cursorial (ground-up) theory. A, the insect-net theory of Ostrom (1979) states that proavians used protowings to catch insects. As the feathers were enlarged for batting insects, the wing motion would turn from swatting into actual flapping flight. B, Caple et al. (1983) proposed that proavians leaped into the air in pursuit of insect prey. Feathers and wings assisted and extended their leaps until flapping flight evolved (after Chatterjee 1997).

sect, *Archaeopteryx*'s wings would need air holes to let air pass, as in a flyswatter. *Archaeopteryx*'s wings did not have air holes; therefore, it would be unable to catch insects in this way. (4) The "insect nets" would have generated several instabilities and loss of balance. All of these problems show that the "insect net" theory cannot possibly work as a step toward flight evolution. If wings really did develop first as insect-catchers, as Ostrom suggests, natural selection would have acted strictly to improve them as flyswatters, not transform their function into flying. Because of these difficulties, Ostrom (1986) later rejected his hypothesis.

Although Ostrom's model has many flaws, it did encourage other groups to revive the cursorial theory, partly because of the phylogenetic relationship of *Archaeopteryx* with dromaeosaurs (Gauthier and Padian 1985; Padian 1985; Sereno and Rao 1992; Ruben 1991). This new version of cursorial theory centers on the premise that the immediate theropod ancestors of birds were strictly terrestrial bipeds that used their wings as bilateral stabilizers during jumps into the air in pursuit of prey. As the jumps lengthened, the wings became increasingly used for balance and propulsion—and the animals began to fly actively without passing through an intermediate gliding stage. As an alternative, Caple et al. (1983) proposed a "fluttering model" (fig. 12.9B). According to these authors, the protobirds might have used their jaws to catch prey but employed their wings as bilateral stabilizers during a jump into the air. Caple and colleagues maintained that the rudimentary wings of protobirds were effective for balance while running, jumping, and turning, until they were able to take off at high speed. They speculated that when the protobirds extended their forelimbs, minute increments of lift made it easier to jump farther and cap-

ture more prey. The motion of the forelimbs for stabilization, according to them, would mimic the flight stroke of a bird. Eventually, the protobirds evolved larger airfoils that enabled them to obtain even greater lift. Also, as lift increased it aided in landings. Therefore, the protobirds could slow down and direct their landings. As a result, power flight evolved (fig. 12.9B).

It is not clear why selection should favor flapping wings for foraging in a terrestrial animal. In the fluttering model, as soon as the protobirds jumped into the air, they would lose airspeed and fall down. Flight at slow speed is aerodynamically more sophisticated and complex than is flight at high speed. It is unlikely that early birds acquired this sophisticated slow-speed flight at the beginning. Foraging in flight requires very fine coordination between the senses and muscles, implying instability and a great degree of maneuverability. It is unlikely that such fine control developed in jumping protobirds with a long stabilizing tail.

Another version of the cursorial hypothesis is that the immediate ancestors of the birds, such as the maniraptoran theropods, were fully terrestrial, their forelimbs being used to subdue and kill prey—these predatory motions are viewed as giving rise to the flight stroke (Gauthier and Padian 1985; Padian and Chiappe 1998). There are several inconsistencies in the prey-catching scenario of the maniraptorans, with their specialized swivel wrist joint (fig. 12.10A). Development of the semilunate carpal, an avian type of linkage system between the elbow and wrist joints, came about in the maniraptorans. As the elbow folded, the hand of the forelimb would have moved farther away from the mouth so, like modern birds, the hands of dromaeosaurs could not be used for predation and feeding. The predatory movements of the forelimbs would be directed forward to grasp the prey, whereas flight movement is essentially dorsoventral; it is inconceivable that this propalinal motion of the hand gave rise to dorsoventral flight strokes. The hands of dromaeosaurs were doing something other than catching prey. As in extant birds, they could be folded at the sides of the body during terrestrial locomotion. The elongated forelimbs and swivel wrist joints in the maniraptorans are interpreted as features evolved for climbing (Chatterjee and Templin 2004a). A longstanding criticism of the cursorial theory is that large, complicated structures such as wings must have evolved all at once from running to flapping, in one great evolutionary lunge without any intermediate stages.

The latest version of the cursorial theory views *Archaeopteryx* as being capable of takeoff from a running start, using its wings as a primary thrust generator (Burgers and Chiappe 1999; Chiappe 2007)—on beginning to run, starting to flap vigorously, gaining considerable velocity from its wing thrust, and taking off. It was proposed that generation of thrust, but not lift, was crucial during ground takeoff (fig. 12.10B). Thrust would have reduced ground traction so much that running speed would have declined. However, there are inconsistencies in the WAIR model. For example, during fluttering of wings, the ground effect would increase lift, not thrust, but decrease the ground traction given by the feet, and acceleration would be lost. A running theropod that flapped its arms would increase drag: the faster the run, the greater the drag. Only the arms would have generated a very small amount of thrust in the early stages of the process. Moreover, there are biological limitations to generation of the vigorous flapping required by *Archaeopteryx* to take off, for example, lack of a modern avian supracoracoideus pulley, the primary elevator of the wing—necessary for rapid wing upstroke (Poore et al. 1997). With a limited upstroke, *Archaeopteryx* would not be able to execute the powerful downstroke necessary to generate sufficient thrust for a ground takeoff. Its flight apparatus was weakly developed compared with that of modern flying birds. For example, the coracoid was too small to produce a wide range of flapping motion and its sternum, the site of attachment of the flight muscles, was not ossified. Its pelvis, synsacrum, and hindlimbs were primitively developed and were not sufficiently strong enough to generate the powerful leg thrust required for a ground takeoff (Chatterjee and Templin 2003). Moreover, its narrow and solid primary rachises suggest poor flapping ability (Nudds and Dyke 2010).

Using a computer simulation model, we showed that

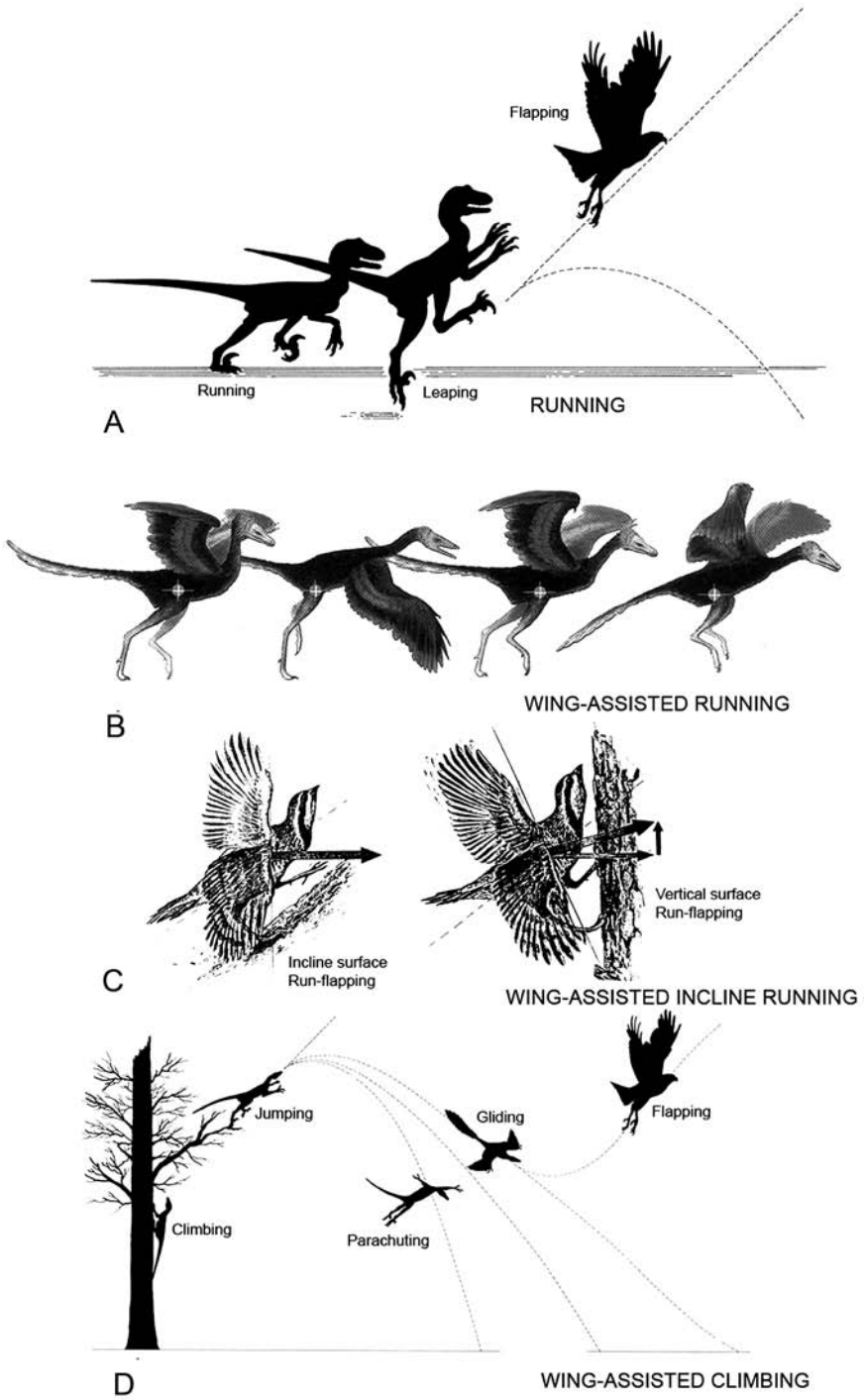


Figure 12.10. Four models for the origin of avian flight. A, the cursorial (ground-up) theory is based on the idea that the proavian was essentially a running theropod that leaped up into the air and became an active flier without any gliding stage. B, the wing-assisted running (WAR) model of cursorial theory showing the takeoff sequence of *Archaeopteryx*, where running speed increases with thrust generated by the wings so the bird begins to take off (simplified from Burgers and Chiappe, 1999). C, the wing-assisted incline running (WAIR) model; a partridge climbs a steep slope by flapping its wings to aid traction, generating a force perpendicular to the plane of wing movement (simplified from Dial 2003). D, the wing-assisted climbing (WAC) model of arboreal theory; a protobird began to climb a tree, assisted by clawed wings to evade predators; in an arboreal lifestyle it began to parachute with its small wings, then glide using gravity as source of power. With the development of large wings, the animal could flap to remain airborne. In the arboreal theory, gravity is used as a source of power to convert potential energy into kinetic energy (after Chatterjee and Templin 2012).

for *Archaeopteryx*, takeoff would have been more efficient and cost effective from a perch than from the ground (Chatterjee and Templin 2003). If *Archaeopteryx*, with its fully developed wings and airworthy feathers, found a ground takeoff difficult, how could the ancestors of the birds, with their fledgling wings, generate sufficient power to become airborne from the ground without the supracoracoideus pulley?

The cursorial theory is based on the assumption that protobirds were obligatorily terrestrial until after the evolution of active flight. This view became no longer tenable as evidence for the arboreal lifestyles of the feathered coelurosaurs from China began to emerge (Zhang et al. 2002; Xu et al. 2003; Chatterjee and Templin 2004a, 2012). The cursorial theory does not adequately explain the origin of encephalization and the neurosensory specializations associated with three-dimensional perceptual control or the transition between rudimentary and fully developed flight (Bock 1985). In summary, biomechanical, neurological, and paleoecological studies fail to support the cursorial theory. In contrast, the fossil evidence supporting the arboreal theory is overwhelming, as discussed below.

Taking off requires more energy than steady level flight because the bird must accelerate and climb. Whenever birds take off from the ground, they need speed to become airborne. It is the speed with respect to the air that matters, not the speed with respect to the ground. The bird must beat its wings more vigorously to obtain the extra lift it needs. Taking off from the ground is hard work that requires four times as much power as ordinary flight (Tennekes 1996). For this reason, most birds prefer to take off from elevated objects such as a tree, a telephone pole, a windowsill, a roof ledge, or a cliff to secure the needed lift. As soon as the protobirds jumped into the air from the ground, they would lose airspeed and altitude and fall back to the ground. There was no lift or thrust to keep them aloft. The cursorial theory, even in its modified form, is biomechanically untenable.

The strongest criticisms against the cursorial theory are based on ecological, adaptive, and mechanical grounds (Jerison 1973; Rayner 1979, 1985, 1988, 1989, 1991; Bock 1983, 1985, 1986; Martin 1983b; Feduccia 1980, 1996, 2012; Norberg 1985, 1990; Pennycuick 1986). There are no contemporary analogues of cursorial bipeds using forelimbs for stability; outstretched wings would increase drag and slow down locomotion. In contrast, modern cursorial mammals such as kangaroos and kangaroo rats have forelimbs that play a passive role during jumping. To minimize the drag force, they are kept in a folded position in a strictly sagittal plane during takeoff, midway through the leap, and during landing (fig. 12.11). Thus, the use of forelimbs for jumping is minimal in these animals and does not mimic a rudimentary flight stroke. As a consequence, selection has favored relatively shorter forelimbs in these animals, quite opposite the trend proposed by Caple and associates. If their model were correct, we would expect to see the emergence of flying kangaroos from their ground-bound ancestors.

The cursorial theory fails to explain fully why the primary vanes of *Archaeopteryx* are so asymmetrical and complex, a condition seen only in modern volant birds. If *Archaeopteryx* were a ground-dwelling bird, as Ostrom depicted, it would have had hair-like feathers, like those of ostriches and rheas. The cursorial theory works against gravity and is energetically more expensive. The effects of gravity would create additional stress on protobirds during takeoff. To overcome this added stress, the supracoracoideus pulley system would be required during takeoff; its lack in *Archaeopteryx* indicates that it took off from trees to become airborne, not from the ground (Chatterjee and Templin, 2003).

The cursorial theory does not address the necessary transitional form between the preflight stage and the active, flapping flight stage; flight would thus have evolved rapidly, from jumping to active flying, almost by saltation without any intermediate gliding stage. This theory does not explain adequately the origin of feathers, endothermy, or brain enlargement and three-dimensional perceptual control. These are important characteristics of birds that must be accounted for in any evolutionary and adaptive model of flight. In the cursorial model, landing was perfected first, followed by improvement of the flight apparatus. In the fossil record of Mesozoic birds,

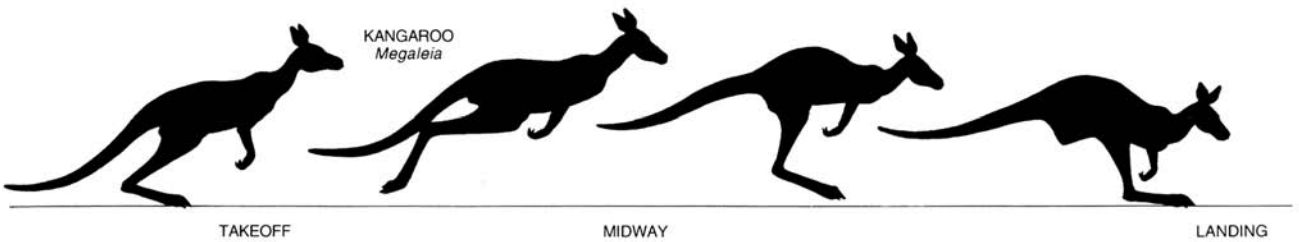


Figure 12.11. Kangaroos (*Megaleia*) share with theropods several functional traits, such as obligate bipedality, cursorial posture, short forelimbs, and a long tail; they offer a modern analogue for testing of the cursorial theory. Successive jumping stages of the kangaroo show a great range of flexion and extension of the hindlimbs. The forelimbs, however, are held close to the body in a parasagittal plane without any activity. It is unlikely that jumping theropods would extend their forelimbs to become fliers because they would thus create drag forces. The origin of flight from the ground up is biomechanically untenable (after Chatterjee 1997).

we see the opposite trend: flight evolved first, followed by the development of avian-style terrestrial locomotion and landing (Chiappe 1995a).

The Wing-Assisted Incline Running Model

In an interesting experiment, Dial (2003) showed that hatchlings of many living ground-dwelling birds, such as the chukar partridge (*Alectoris chukar*), tend to seek refuge at heights when threatened (fig. 12.10B). They vigorously beat their wings to run up steep slopes of 45°, even vertical substrates, increasing the load on their hindlimbs to reach these heights. As they run uphill, the chukars flap their wings strongly up and down at a different angle from that used when flying, thus improving the traction of their legs on the vertical surface. After trimming the remiges of chukars of various ages, Dial demonstrated that without feathers, the birds could not run up slopes steeper than 60°. In contrast, fully feathered chukars could climb vertical substrates. Dial thus concluded that flapping does not lift the bird, but rather the opposite: it presses the bird into the inclined surface to increase its traction, to keep its feet from slipping, "acting like the spoiler on a racing car" (Dial 2003, 403). Later, Bundle and Dial (2003) performed experiments on a number of chukars using two accelerometers to measure the acceleration in the forward and vertical directions. They concluded that vertical ascent is possible for a chukar when it simultaneously flaps its wings and runs on its legs.

Although Dial has discovered a novel method by which poorly flying birds can get off the ground, its relevance to the origin of avian flight is unclear at the moment. Bundle and Dial (2003) acknowledge that the behavior they observed in young partridges is not necessarily the basal condition of birds or their ancestors. They believe that this climbing behavior of the partridge is an escape strategy. Lacking a supracoracoideus pulley and a keeled sternum, the protobirds, such as the feathered dromaeosaurs and *Archaeopteryx*, could not perform these complex wing movements to generate the thrust required for a vertical ascent, as proposed by Dial. It appears that the WAIR motion involves fully developed wing movement and is only possible when birds have learned how to perform complex wing movements, after acquiring the supracoracoideus pulley, which was absent in *Archaeopteryx* and its immediate ancestors (Poore et al. 1997). Most climbing vertebrates do not use WAIR to reach heights. It is unlikely that the protobirds could generate enough thrust against gravity to prevent slipping from vertical substrates; they must have used their claws to cling to tree trunks. In fact, Dial (2003) has shown that the young partridge moves its wings differently when climbing steep slopes than when it flies.

The ability of a young partridge to climb vertical surfaces is a twist on the arboreal theory, in which initial height must be gained by climbing before the bird launches from a perch. The WAIR model does not specify how early birds took to the air. It fails to explain why the protobirds and *Archaeopteryx* retained a grasping hand equipped with sharp and recurved claws, if the wings were not used for climbing. To understand the origin of

avian flight, a scansorial baby hoatzin is a better analogue than a chukar because its hands are equipped with sharp claws supported by elongated penultimate phalanges, like those of the protobirds and *Archaeopteryx*, for grasping cylindrical vertical trunks. The wing-assisted climbing (WAC) adaptation, as discussed in the following section, is prevalent among hoatzin chicks, which crawl and clamber through tree branches with their wing claws, just as protobirds might have done millions of years ago (fig. 12.13A, B). Their grasping hands, with swivel wrist joints and terminal claws, are exceedingly similar to those of the maniraptoran coelurosaurs. The claws, which persist in the inner fingers (1 and 2) for the first three months of life, are absent in adults but provide youngsters with just the extra grip they need to climb back up to the nest area (Chatterjee 1997). Much anatomical evidence supports the WAC adaptations of the protobirds, such as the laterally facing glenoid, elongated forelimbs, semilunate carpal with a swivel wrist joint, elongated penultimate phalanx, and sharp recurved claws, as in the young hoatzin, which are typical of trunk-climbing birds (Chatterjee and Templin 2003, 2004a). Feduccia (1993) suggests the proportions and curvatures of the manual phalanges of *Archaeopteryx* attest to its climbing ability. The lengths of the proximal and penultimate phalanges differ among terrestrial and scansorial birds. The penultimate phalanx, which supports the claw, is longer than the proximal phalanx in scansorial animals, which increases the diameter of the grasping hand. If the wings were used solely for WAIR flapping motion by the early birds, elongated penultimate phalanges and sharp claws would be superfluous in those animals. Their presence attests to their adaptation to WAC, not WAIR, during the evolution of true flight. Moreover, the lack of fusion or rigidity in the critical regions of the pelvis, synsacrum, tibiotarsus, and tarsometatarsus indicates that feathered coelurosaurs similar to those from China (the presumed ancestors of birds) were not specialized for running uphill like a chukar (Chatterjee and Templin 2003). Most of these coelurosaurs had arboreal habitats, as discussed below. This new anatomical and ecological evidence is in serious conflict with the WAIR model of flight.

The Arboreal Theory

The arboreal theory begins with small, wing-assisted climbing protobirds that began to leap from branch to branch, then to parachute by spreading their forelimbs to increase their resistance and to slow their descent, then to glide, and finally to fly with wing strokes. The central theme of the arboreal theory is the use of gravity as a source of power by the protobirds to convert potential energy to kinetic energy.

Charles Darwin (1859) was probably the first to propose the arboreal theory for the origin of bats, and Othniel Charles Marsh (1880) extended this idea to birds. Marsh observed that a large number of Holocene birds lived in trees or bushes and that there are many modern parachuting and gliding tetrapods, all of which are arboreal. Marsh believed that flight evolved from arboreal protobirds whose scales developed into rudimentary feathers. These feathers were used as parachutes, slowing the descent of the animals as they leaped from branch to branch and controlling their jumps and falls.

In 1926, Gerhard Heilmann argued strongly in favor of the arboreal theory. Like Nopsca, he also believed that the protobirds were bipedal animals. Heilmann developed an adaptive model where ground-dwelling runners became tree-climbers. Once in the trees, the protobirds would leap from limb to limb. They would start leaping from low branches to the ground and eventually begin to glide. As gliding became specialized, active flight would evolve. Heilmann thus set the stage for the arboreal theory that was later refined by other workers.

Walter Bock (1965, 1969, 1983, 1985, 1986) presented a more detailed version of the arboreal theory in the context of the historical narrative, which means that earlier events affect later ones. Bock reconstructed the life history of protobirds from recent examples of birds. He believed that protobirds spent some time ground feeding and the rest of the time sleeping, hiding, and nesting in trees. He argued that protobirds climbed trees with the aid of manual and pedal claws. Once they became more confident in climbing, they would jump from limb to limb and make short jumps to the ground to conserve

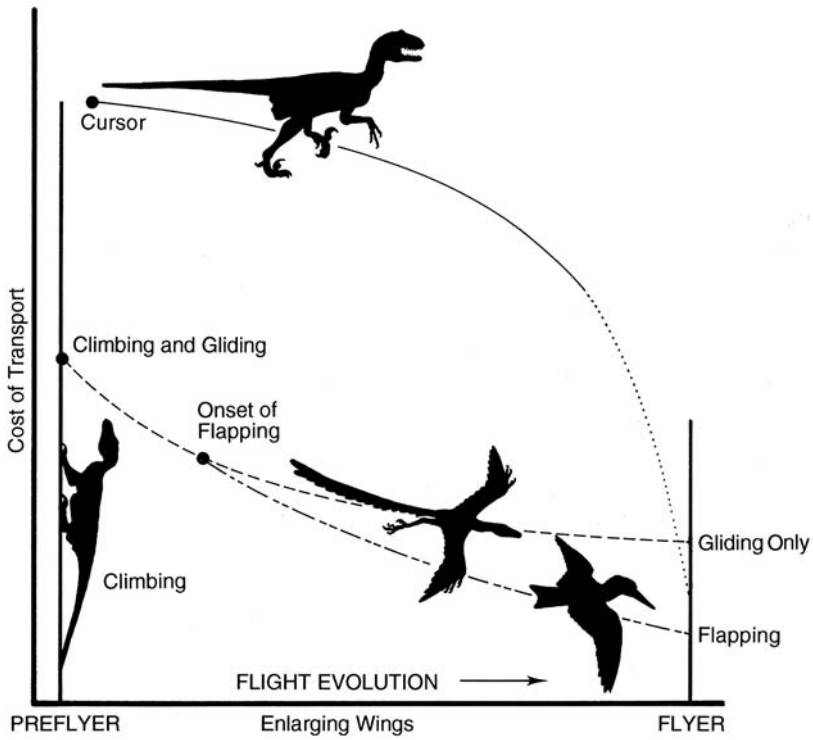


Figure 12.12. An energy-saving mode of locomotion. It costs less for a protobird to climb a tree and then glide or flap its wings than to run (after Chatterjee 1997).

energy and time. The next step would be to make longer jumps or to parachute, which was an unspecialized glide with a steep angle of descent. As the angle of descent decreased to less than 45°, gliding would commence (fig. 12.10D). Gliding is a more efficient way to travel over horizontal distances than is walking or running (fig. 12.12). Gliding also increases maneuverability and slows down landing. These three actions—climbing, parachuting, and gliding—were important because they allowed flight muscles to become powerful. Once gliding became specialized, flapping could begin. The initial gliding flight would obtain energy from gravity. Bock suggested that flapping began when protobirds were landing. Flapping would add additional power, thus prolonging flight and reducing the energy cost of transport.

Chatterjee (1997) and Chatterjee and Templin (2003, 2004a, 2005, 2007, 2012) revived the arboreal theory in a theropod phylogenetic framework using biomechanical and paleoecological interpretations of the Chinese feathered coelurosaurs. Most recent researchers of avian flight now support this new version of the arboreal theory, which is further elaborated here, supplemented with new evidence (Elzanowski 2002; Paul 2002; Xu et al. 2003; Zhang et al. 2002, 2008). Even Chiappe (2007), a staunch supporter of the cursorial theory, has endorsed our arboreal model as a plausible sequence by which flight in birds might have arisen.

Although the arboreal theory is intuitively more attractive because it makes use of gravity to power flight, a combination of phylogenetic, paleoecological, adaptive, functional, and aerodynamic evidence is presented here to resolve the longstanding question on the origin of flight. The strongest evidence in favor of arboreal theory comes from the Chinese feathered coelurosaurs that represent critical transitional stages in the origin of flight. I propose a modified version of the arboreal model in the context of recent theropod phylogeny. Climbing and arboreal adaptations of feathered coelurosaurs from China, their subsequent enlargement of the brain in a three-dimensional arboreal setting, and acuity of vision were ideal preflight

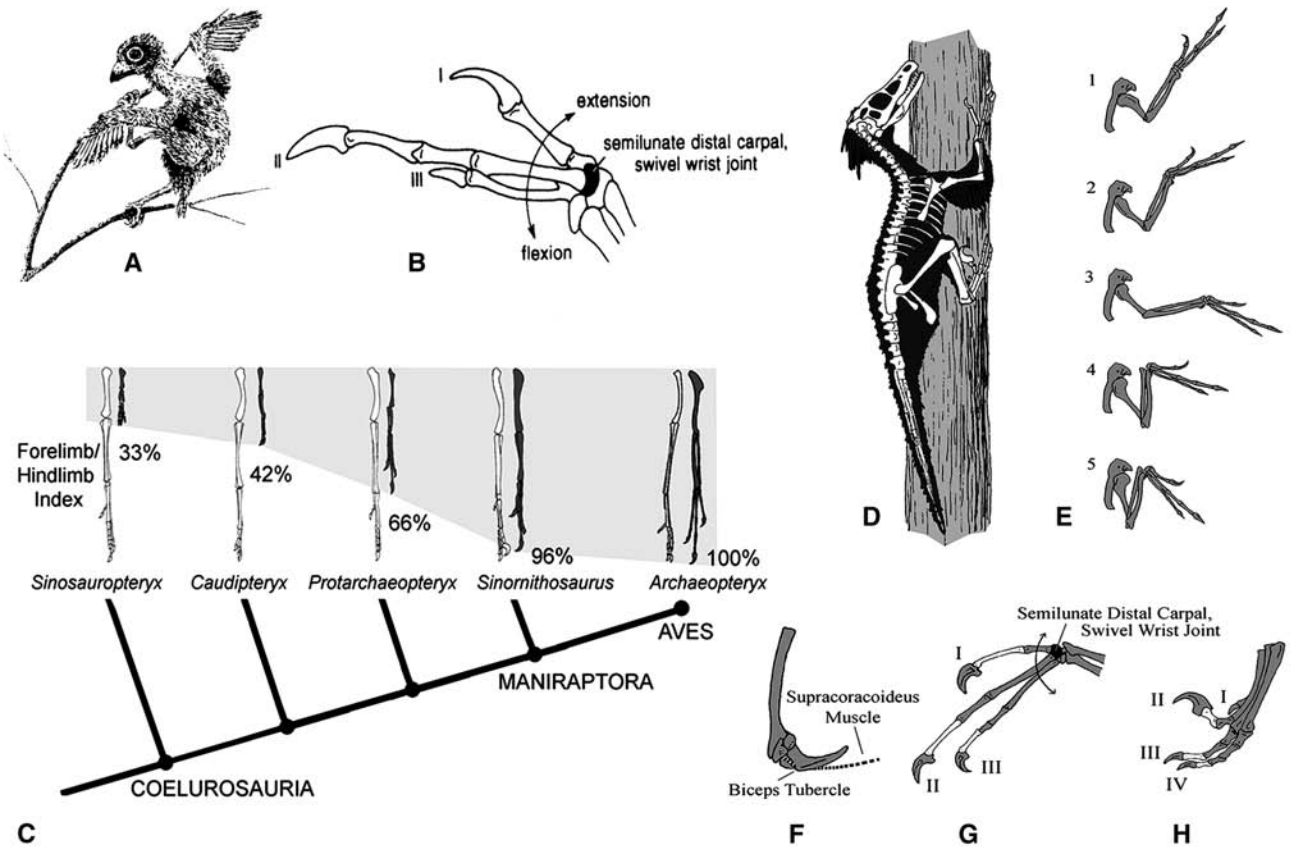


Figure 12.13. Wing-assisted climbing (WAC) adaptations. A, illustration of a hoatzin (*Opisthocomus*) chick climbing trees with its wing claws. B, hand of a young hoatzin showing the swivel wrist joint and terminal claws used for climbing trees. C, diagram showing gradual lengthening of the forelimbs in relation to hindlimbs in arboreal coelurosaurs, initially for climbing and later for flying. D, climbing adaptations of maniraptorans such as *Sinornithosaurus*, including elongated forelimbs, swivel wrist joints, and recurved claws for grasping trunks, a caudally directed pubis, and a stiffened tail as a supporting prop. E, sequence of a synchronized forelimb cycle (1–5) employed during climbing—precursor to flight strokes: up-and-forward and down-and-backward. F, shoulder girdle showing the laterally facing glenoid for dorsoventral wing excursion and a biceps tubercle for the inception of the acrocoracoid process. G, grasping hand with a longer penultimate phalanx and recurved claws for hooking and clinging to trunks. H, pes, showing sharp claws for anchoring to tree trunks (after Chatterjee and Templin 2012).

training. The selective payoff of the successful mastery of flight motions—parachuting, gliding, and flapping—gave significant advantages to early avialans over their terrestrial counterparts.

Wing-Assisted Climbing

Birds acquired two independent and specialized methods of locomotion: walking with their hindlimbs and flying with their forelimbs. During the evolution of flight in the transition from theropods to birds, the hindlimbs did not change significantly. The forelimbs underwent progressive structural and functional modifications as they evolved into wing-like structures, in the transition from grasping to climbing to balancing to parachuting to gliding to flying. These adaptive modifications were accompanied by a gradual lengthening of the forelimbs relative to the hindlimbs in the same way as in coelurosaurs, to increase the wingspan, so that the forelimbs and hindlimbs became equal in length (fig. 12.13C) (Chatterjee 1997; Chatterjee and Templin 2004a, 2007, 2012). Simultaneously, the feathered coelurosaurs became relatively small; life in the trees would favor the smaller size of animals. Small size

has several advantages, including reducing the energy expended for vertical climbing, allowing support by smaller branches, and reducing impact force when hitting the ground during accidental falls from trees. Small size could also be associated with insulation of the body by feathers and may constitute a prerequisite for the early evolution of flight (Bock 1985). In maniraptorans, with the development of long hands, a swivel wrist joint (fig. 12.13D), a stiffened tail, an ossified sternum, a biceps tubercle, and a streamlined body (opisthopubic pelvis), the scansorial, or climbing, adaptation on a vertical tree trunk is perfected. The synchronous forelimb motion used during climbing would mimic a rudimentary flight stroke. The animals could possibly parachute and glide from treetops with the development of the patagium in the proximal part of the forelimb (fig. 12.14A).

The best evidence that climbing vertebrates can learn to power fly is provided by pterosaurs and bats; pterosaurs probably climbed two-dimensional sea cliffs, whereas bats scaled three-dimensional trees, as reflected by their brain architecture (Jerison 1973). Thousands of species of amphibians, reptiles, birds, and mammals are climbers, demonstrating that scansorial adaptation is a viable mode of life. These animals not only climb, but also some of them leap among branches and others glide. Climbing on vertical substrates is a difficult endeavor, and the protobirds required two abilities to overcome this problem (Hildebrand 1982). They needed mechanisms to avoid falling from trees, and they had to propel themselves on tree branches, a discontinuous, three-dimensional substrate with variable width and orientation. Because the tail was used for bracing in climbing protobirds, the function of the *M. caudofemoralis longus* muscle changed from femoral retraction to tail depression. The dorsoventral movement of the rigid, stiffened tail, used as a prop in climbing, would act as an aerodynamic stabilizer during gliding to change the pitch axis and extend the gliding path (fig. 12.14A).

Maniraptorans such as *Caudipteryx* probably climbed trees quadrupedally like tree kangaroos and cats, grasping the tree trunks with arms out to the sides and the flexed legs close to the body. They display characters for climbing vertical trunks, such as the laterally facing glenoid for dorsoventral humeral excursion, a biceps tubercle for inception of the supracoracoideus tendon, elongated forelimbs for grasping trunks, ossification of the sternum for attachment of the pectoralis and supracoracoideus muscles, swivel wrist joints to allow movement of the hands in the plane of the forearms, longer penultimate phalanges and recurved claws for grasping and hooking onto trunks, a caudally directed pubis to flatten the body, and a stiffened tail as a supporting prop (Chatterjee 1997; Chatterjee and Templin 2004a). They acquired various structural adaptations for clinging, hooking, and bracing to avoid falling from vertical substrates. They climbed with wings, feet, and tail. They had shorter bodies and longer limbs, with grasping hands. The claws of both hands and feet were highly recurved, similar to those of tree-climbing birds, so that they could be dug securely into the bark. In climbing a vertical trunk, the outstretched forelimbs were pressed against the lateral side of the trunk, while recurved claws provided a hooking grip. The body was held in a vertical position without much undulation. The sharp, recurved claws allowed adduction force to keep them embedded in the bark. They helped to secure the grip during climbing and supported part of the body weight (fig. 12.13G). Presumably protobirds used their limbs alternately in unison, first the paired forelimbs and then the paired hindlimbs. Modern flying squirrels climb rapidly in this manner. Numerous trunk climbers use their tails as braces, struts, or props. The maniraptorans had a rigid tail that could have served as a prop during climbing, as in woodpeckers, to support part of the body weight (fig. 12.14B). The presence of feathers in the tail might have enhanced the function of the tail as a stiff prop by increasing friction between tail and tree (Paul 2002).

The climbing movement of birds (Stolpe 1932) and primates (Cartmill 1985) on a vertical trunk has been studied in detail. Using these modern analogues as a guide, we can speculate about the scansorial ability of protobirds. In climbing a tree, a proavian would work against gravity, and the role of friction was important in the prevention of slipping. A free-body diagram shows the action

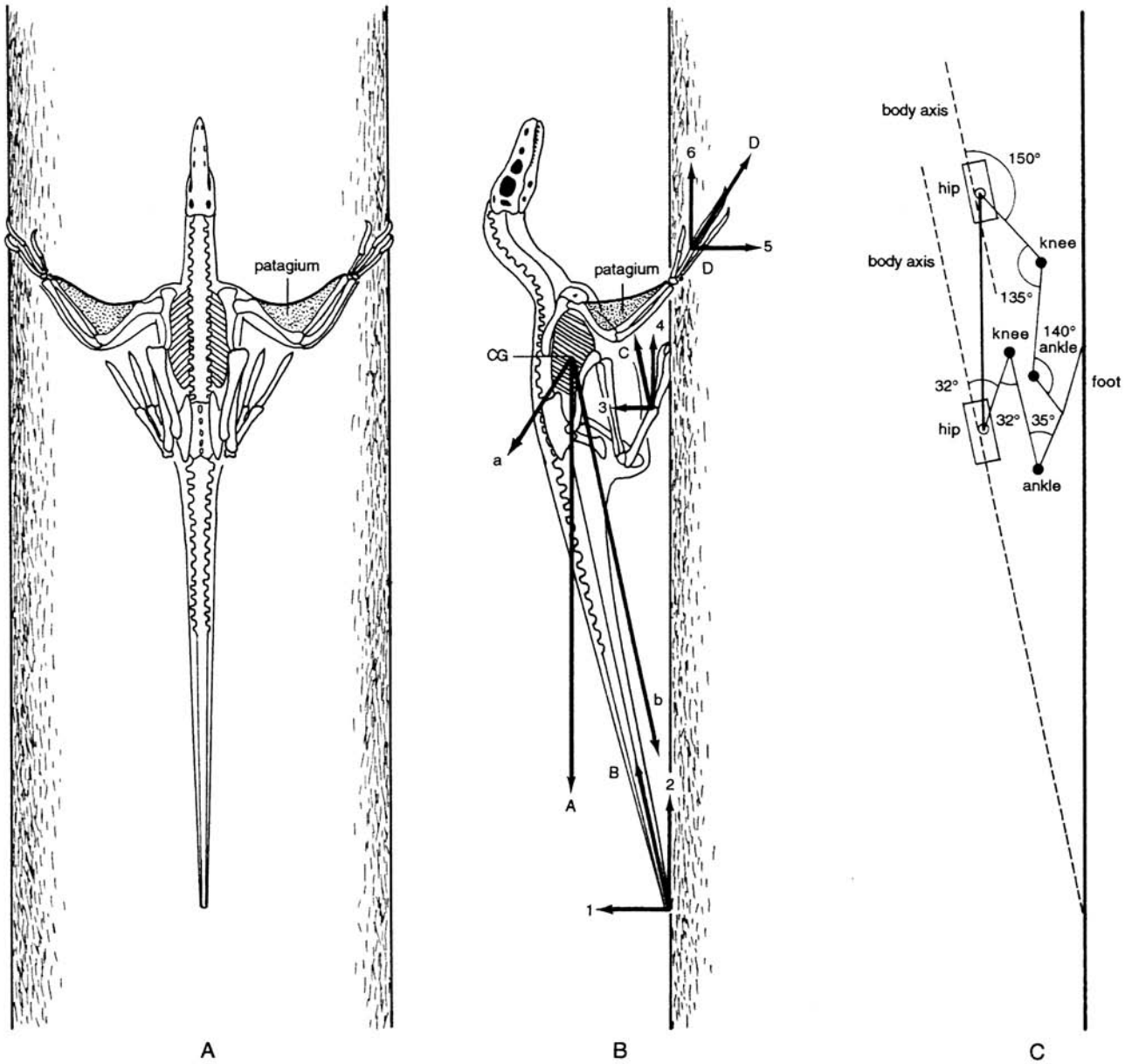


Figure 12.14. Scansorial adaptation of a small maniraptoran such as *Caudipteryx*. A, dorsal view of the climbing maniraptoran, clinging quadrupedally to a vertical trunk; the patagium might have developed in front of the elbow as an elastic strap to keep the body close to the trunk; B, free-body diagram of the climbing maniraptoran in equilibrium in the right lateral view. The force of gravity A is acting on the animal along the center of gravity (CG) and is counterbalanced by forces at three points: B (tail), C (foot), and D (hand). 1 to 6 are components of these forces. When the system is at rest, the sum of all translation forces must be zero (vertical: A = 2 + 4 + 6; horizontal: 1 + 3 = 5). C, stick diagram of maniraptoran in the right lateral view showing the climbing sequence; the positions of only the hip and hindlimb segments are shown. As the hindlimbs are unfolded, feet provide the thrust that propels the body upward. In this position, the femur retracts considerably, about 150° from the body axis, and the knee and ankle joints are extended (after Chatterjee 1997).

of forces on a climbing proavian clinging quadrupedally to a vertical support (fig. 12.14B). The force of gravity, A, was acting on the animal along the center of gravity (CG) and was counterbalanced by forces at three points, B (tail), C (foot), and D (hand). Forces a and b were two components of those opposing forces. Force a was directed downward and inward parallel to the axis of the tail and would be counterbalanced by a combined action of forces B (provided by the tail) and C (by the pes). The outward component of A, force a, tended to topple the animal away from its support and was counterbalanced by force D at the hand. When the proavian was at equilibrium, the sum of all translation forces would be zero (vertical: A = 2 + 4 + 6; horizontal: 1 + 3 = 5).

The sequence of limb kinematics of protobirds during the propulsive and recovery phases of climbing is interesting. The forelimbs and hindlimbs moved in a reciprocal manner. In the recovery phase, the forelimbs were outstretched and swung upward and the manus was extended to grasp the cylindrical trunk; the weight of the body was carried by the highly flexed hindlimbs (fig. 12.14C). In the next propulsive phase, the hands and the forelimbs were gradually flexed to propel while the hindlimbs were extended to move the animal upward. The highly flexed hindlimbs provided much of the propulsive thrust. The swivel wrist joint and lengthening of the forelimbs in protobirds were obvious adaptations that facilitated the climbing of vertical trunks.

Arboreal theory helps to explain the evolution of the locomotor module of birds. Basal theropods, such as ceratosaurs, were obligatory bipeds with forelimbs decoupled from terrestrial locomotion, used for the capture and manipulation of prey. They possessed a single locomotor module, which included the hindlimbs and tail. Contrastingly, extant birds have three locomotor modules: hindlimbs, forelimbs, and a tail, with the latter two acting in concert during flight. The evolution of three locomotor modules in birds can be traced from terrestrial single-modular ceratosaurid locomotion through the three-modular vertical climbing of maniraptorans. Without transitional climbing and gliding stages, the transformation of the primary nonlocomotor forelimbs of theropods into aerodynamic flight surfaces for flight in early birds is abrupt and difficult to explain in the context of terrestrial theory.

Ancestral birds may have climbed the vertical trunks of trees in a way similar to that of modern flying squirrels—using their limbs alternately in unison; first the paired forelimbs and then the paired hindlimbs, using their clawed hands and feet as crampons and their rigid tail for additional support. While climbing, the outstretched forelimbs were pressed against the sides of the trunk, recurved claws providing a hooking grip; the forelimbs and hindlimbs moved in a reciprocal manner. In the recovery phase, the forelimbs were outstretched and swung upward, while the manus were extended to grasp the trunk. The weight of the body was carried by highly flexed hindlimbs. In the next propulsive phase, the hands and forelimbs were gradually flexed to propel the animal, whereas the hindlimbs were extended to move the animal upward. The highly flexed hindlimbs provided much of the propulsive thrust, while the swivel wrist joints helped the hands to bend to accommodate this upward movement. The sequence of such a strong, synchronized forelimb cycle during climbing was a precursor to a flight stroke: up-and-forward and down-and-backward (fig. 12.13E). This climbing transition allowed the forelimb to eventually gain a novel function within the coelurosaurs: flight. Such an increase in modularity, from one to three modules, made birds champions in exploiting a different ecospace and adapting a wide range of lifestyles.

Several of the new Chinese paravians exhibit obligatory arboreal habits, suggesting that trees became "safe havens" for these dinosaurs. For example, scansoriopterygids such as *Epidendrosaurus* (Zhang et al. 2002) and *Epidexipteryx* (Zhang et al. 2008) from the Middle to Late Jurassic of Inner Mongolia had developed WAC hands with curved claws and extremely elongated third fingers, possibly for probing for insects in trees. In these animals, the forelimbs are longer than the hindlimbs, the toes show long penultimate phalanges, and perching feet have a reversed hallux and highly recurved pedal claws for grasping branches, features associated with arboreal adaptation. Another closely related form exhibiting

similar obligatory arboreal adaptations is *Scansoriopteryx* (Czerkas and Yuan 2002). *Epidendrosaurus*, *Epidexipteryx*, and *Scansoriopteryx* lacked any flight feathers, and became secondarily flightless, but remained arboreal for safety, probably because of their diminutive size. They developed fluffy down feathers as they reverted to flightless, arboreal forms (fig. 3.17).

In contrast, other arboreal forms from China, such as *Anchiornis* from the earliest Late Jurassic of Liaoning Province (Hu et al. 2009), *Microraptor* (Xu et al. 2003) and *Sapeornis* (Gao et al. 2012) from the Early Cretaceous of Liaoning Province, and *Pedopenna* (Xu and Zhang 2005) from the Middle to Late Jurassic of Inner Mongolia, developed long contour feathers along the entire length of the metatarsus (fig. 12.18A); these feathers extended below the level of the feet, thus hindering terrestrial locomotion. The presence of large metatarsal feathers in the tetrapterygids, such as *Microraptor* and *Anchornis* and in the pygostylian *Sapeornis* indicates their obligatory arboreal habitat (Zheng et al. 2013). Recent discovery of arboreal enantiornithine birds in the stomach contents of *Microraptor* provides additional support to interpretations that *Microraptor* was spending a substantial amount of time in the trees to capture arboreal birds (O'Connor et al. 2012). It is likely that *Jeholornis* and its immediate ancestors were arboreal and began flying from trees.

Neurosensory Evidence

The abundance of plant remains found in association with the feathered coelurosaurs and early avialans is consistent with their being dwellers in the forest environments of Liaoning. In addition to ecological evidence, the enlargement of the brain in these feathered coelurosaurs suggests their arboreal lifestyle. Because impressions found in endocasts can reveal relative brain sizes and surface features, such as the boundaries between the brain components (cerebral hemispheres, optic lobes, and cerebellum), gross aspects of the theropod brain architecture can be compared with those of living reptiles and birds. The architecture of the brains of coelurosaurs, their relatively large brains, and their visual acuity are good indicators of arboreal habitats (Jerison 1973; Chatterjee 1997). Compared with all the other dinosaurs, the coelurosaurs have larger brains (Hopson 1980) and larger eye sockets, possibly in response to a new set of selection pressures in arboreal niches (fig. 3.12). Spending much of their lives in trees, coelurosaurs would have required large brains and refined sensory organs capable of orienting them in the tangle of a tree's branches. They also developed the typical avian architecture of the brain with the cerebral hemispheres expanded for enhanced senses and intelligence and in contact with the cerebellum dorsally—thus displacing the optic lobes ventrally and laterally. Across their phylogeny, avian brains show broad similarities in architecture and internal connectivity. The architecture of the avian brain begins to appear in arboreal coelurosaurs; it is a good index with which to distinguish between terrestrial and arboreal forms of theropods. In typical terrestrial theropods such as allosaurs and tyrannosaurs, the brains were small and the brain architecture had the typical reptilian pattern, with the cerebral hemispheres, optic lobes, and cerebrum arranged serially on the dorsal surface; the intervening optic lobes preclude any contact between the cerebrum and cerebellum (Jerison 1973; Hopson 1980; Chatterjee 1991, 1997).

Brain architecture and vision-related anatomy provide the strongest evidence for the arboreal lifestyle of the coelurosaurs. In the 1970s, Jerison (1973) developed the concept of the encephalization quotient (EQ) as a simple way of measuring an animal's intelligence, working on the assumption that smarter animals have larger brain-to-body ratios than less intelligent ones. The EQ measures the size of a creature's brain relative to the size of the rest of its body, and compares this ratio against that of other species of roughly the same size. From 0.25 in the early coelurosaurs, the EQ began to increase considerably to 0.54 in modern birds (Chatterjee 1991, 1997; Chatterjee and Templin 2004a). In contrast, typical terrestrial theropods, such as ceratosaurs and allosaurs, had relatively small brains, with an EQ around 0.15. It is assumed that this was because they lived in a neurologically less-demanding world (Chatterjee 1997). The arboreal ancestral birds required larger brains than terrestrial dinosaurs, just as the earliest primates required larger brains than other mammals

of their time (Jerison 1973). The neurological distinction between arboreal and terrestrial theropods is analogous to that of arboreal cats and terrestrial dogs, the former having a good three-dimensional sense and relatively larger and more complex brains (Bock 1985). Progressive enlargement of the brain and enhanced vision in the coelurosaurs are attributed to invasion of a new adaptive zone, the complex arboreal niches such as those of living primates (Jerison 1973; Chatterjee 1997). The confusingly mottled background of leaves, branches, and other foliage at different levels of trees might have provided a strong selection pressure for enlargement of the brain in order to process complex three-dimensional visual information.

Flight in birds is primarily guided by vision that provides spatial information at sufficient speed and resolution to guide flight. Together with encephalization, the visual resolving power of ancestral birds was greatly improved in aerial niches as is evident by the enlargement of their optic lobes—the major site for visual processing in the brain. The orbits were enlarged and, positioned frontally, resulted in broad, overlapping stereoscopic vision. Vision played a key role in early avian evolution in an arboreal setting.

Arboreal coelurosaurs not only developed visual acuity but also acquired an enhanced auditory system for balance and hearing to supplement their sense of smell—as is evident from the endocasts of the inner ear region containing an elaborate vestibular system and elongated cochlea (Hopson 1980; Chatterjee 1991, 1997). The large vestibular system, the built-in gyroscope required for three-dimensional orientation, is a prerequisite for active flight. Similarly, a well-developed inner ear with an elongated lagena, as seen in the coelurosaurs and modern birds, is associated with hearing acuity and vocal behavior. Refined hearing might have played an important role in such archaic bird activities as communication, alerting others of impending danger, mating, the care of young, and social behavior. A capacity for three-dimensional orientation and hearing acuity would be more likely to have evolved in arboreal animals than in ground-dwellers. The earliest birds depended increasingly on sight and sound and less on smell—as is apparent from their reduced olfactory lobes in endocasts. A sense of smell is less important in arboreal animals.

Feathered Coelurosaurs

In the Daohugou and Jehol biota, nonavian coelurosaurs are presently represented by sixteen genera (fig. 3.10); with new discoveries, the number increases every year. Most coelurosaurs are small—chicken-sized to turkey-sized. Size reduction is a critical step in the origin of flight. To trace the evolutionary sequence of flight, we follow the paleoecological evolution of avialans from their theropod antecedents in an arboreal setting (fig. 12.15). The six taxa listed show transitional stages in the flight apparatus and feather development leading to an *Archaeopteryx*-like wing planform. Phylogenetic analysis has demonstrated that the taxa *Sinosauropteryx* (Chen et al. 1998), *Caudipteryx* and *Protarchaeopteryx* (Ji et al. 1998), *Anchiornis* (Hu et al. 2009), *Sinornithosaurus* (Xu et al. 1999a), and *Microraptor* (Xu et al. 2000; Chatterjee and Templin 2007a) are successively closer to *Archaeopteryx*.

As in Cenozoic birds, recurrent flightlessness was common among archaic Mesozoic birds and their antecedents when they began learning to fly (Paul 2002). We exclude *Beipiaosaurus* (Xu et al. 1999b), a basal therizinosaur, from the flight analysis because it is more than 2 meters long, the largest Liaoning theropod, and may have become secondarily flightless (this is suggested by its filamentous feathers, large size, bulky body, and reduced wings). Secondary flightlessness raises a complex but interesting issue in terms of the origin of flight. How do we differentiate between primary terrestrial coelurosaurs and secondarily neoflightless species that reverted to a terrestrial lifestyle from their arboreal habitats? The answer may be found in the study of modern flightless birds such as ostriches, rheas, and emus. It is generally believed that ratites are secondarily flightless descendants of their flying ancestors, which, after losing their power of flight, evolved into medium-sized grazing animals (Feduccia 1996). The flight apparatus of ratites is a response to their paedomorphic terrestrial adaptation with development of reduced wings, fluffy feathers, a flat sternum, and lack of ossification around the ilioischiadic fenestra.

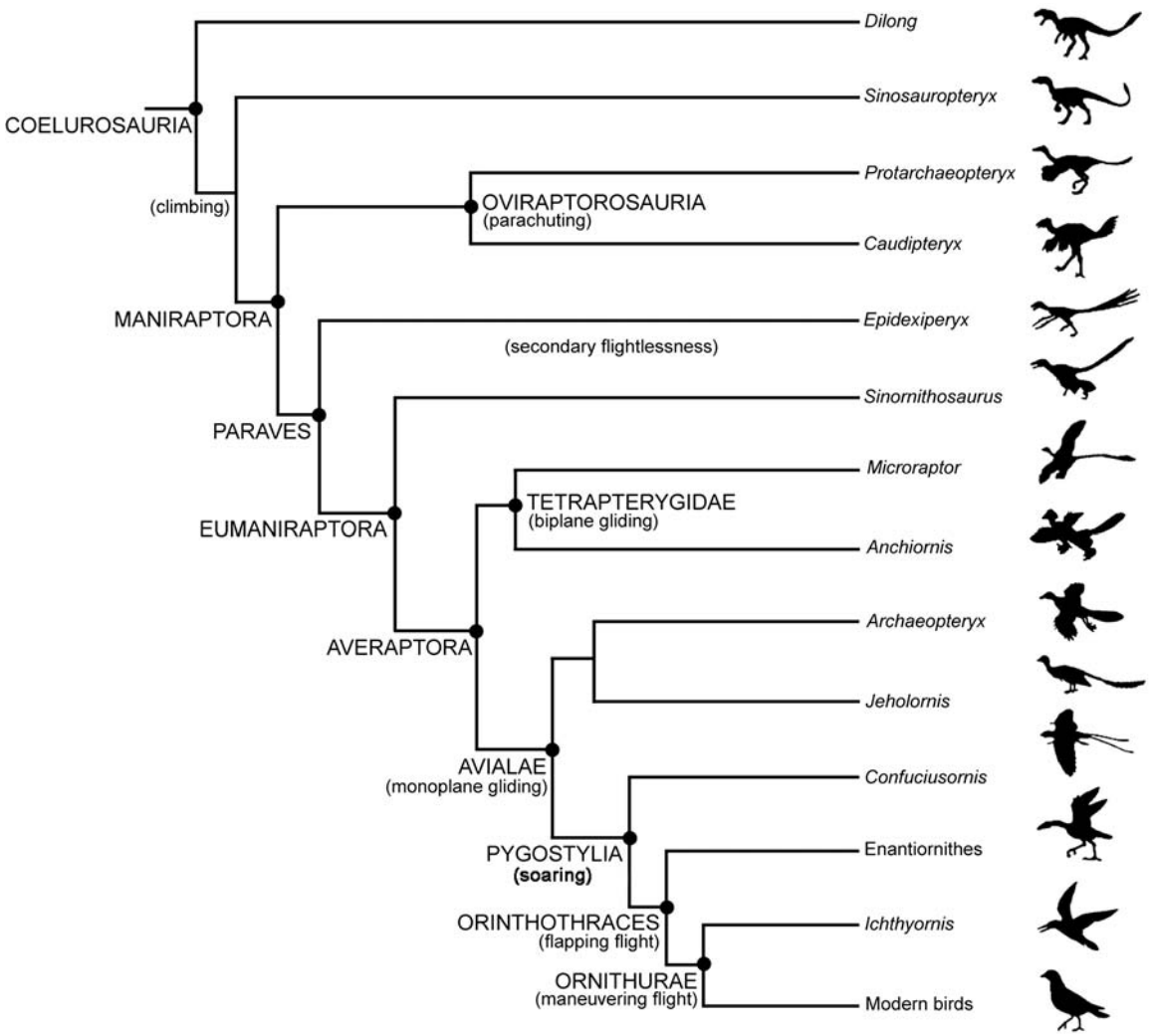


Figure 12.15. Cladogram showing the paleoecologic evolution of birds and their flight. The sequence of events (from climbing and leaping, to parachuting, to biplane gliding, to monoplane gliding, to undulating flight, to flapping flight, to maneuvering flying) are plotted against salient genera involved in the origin of avian flight (modified from Chatterjee and Templin 2012).

However, their brain architecture has retained clues to their arboreal and flying heritage: an encephalized brain, color vision, and acute eyesight (Cornfield et al. 2008). Although ratites have relatively smaller brains and cerebral hemispheres than neognaths, their brain architecture is very similar to that of extant flying birds. Therefore, brain architecture may provide an important clue with which to discriminate between primary terrestrial forms and secondarily flightless groups.

Secondarily flightless coelurosaurs, such as *Beipiaosaurus*, *Deinonychus*, and *Velociraptor*, became large and efficient hunters on the ground but their arboreal heritage is evident in the retention of large brains, big eyes, downy feathers, elongate forelimbs with sharp claws, grasping hands, and stiff tails (Chatterjee and Templin 2004a). In contrast, other large theropods, such as the allosaurs and tyrannosaurs, display no evidence of having passed through an arboreal stage in their early evolutionary history: they appear to have been always terrestrial—this is reflected in their small brains and large bodies (Chatterjee 1997). Because all maniraptorans developed relatively large brains with an avian architecture, they were either

arboreal or became secondarily cursorial from arboreal ancestors. Another secondarily flightless terrestrial form is an oviraptorid, the skeleton of which has been found crouching over its clutch of eggs. Advocates of the cursorial theory have cited this evidence of ground-nesting behavior as supporting the cursorial model (Chiappe 2007). This nesting behavior points to the terrestrial lifestyle of the oviraptorids; they became large and secondarily flightless like some other maniraptorans. Moreover, arboreal nests are less likely to have been preserved in the fossil record and would be difficult to identify.

Some basal avialans such as scansoriopterygids became secondarily flightless but retained an arboreal lifestyle. These flightless forms include *Epidendrosaurus* (Zhang et al. 2002) and *Epidexipteryx* (Zhang et al. 2008) from the Late Jurassic deposits of China and *Scansoriopteryx* (Czerkas and Yuan 2002) from the Jehol Group. They became secondarily flightless when they reverted to downy feathers to become fully arboreal but retained their climbing wings. The living kakapo parrot (*Strigops habrotilus*) of New Zealand, a flightless species, is a modern analogue of Scansoriopterygidae. The kakapo has unusually soft and colorful downy plumage covering its body; it can climb trees and parachute down using its wings for balance and braking. The difference between terrestrial and arboreal flightless early birds—which lost their incipient flying power secondarily—is that the former group has a large body size, whereas the arboreal species became progressively smaller, with highly elongated forelimbs. Along with *Beipiaosaurus*, we have also excluded *Epidendrosaurus*, *Epidexipteryx*, and *Scansoriopteryx* from our performance analysis because these feathered coelurosaurs became secondarily flightless.

Methodology

Much of our understanding of the mechanics of flight in birds is based on analogy with aircraft. Unlike airplanes, flying vertebrates obtain both lift and thrust by beating their wings. In this respect, they are like helicopters, which depend on their rotors for both lift and thrust. In this study, we used helicopter streamtube momentum theory to calculate the flight performances of the prototobirds and early birds. A full account of the method, as applied to animals, is given elsewhere (Templin 2000; Chatterjee and Templin 2004a). Various flight parameters of the coelurosaurs and early birds, such as wingspan, wing area, and body length, were calculated from actual specimens or high-fidelity casts (Chatterjee and Templin 2003, 2004a, 2007, 2012). We digitized the wing margin in its dorsal aspect with a computer program produced by James Rohlf at SUNY Stony Brook and estimated the wing area. We estimated the mass using a multivariate analysis proposed by Atanassov and Strauss (2002). To analyze the flight performance of the coelurosaurs and early birds, we used two computer algorithms, ANFLTPWR (animal flight power) and ANFLTSIM (animal flight simulation), based on the streamtube model (Templin 2000; Chatterjee and Templin 2003, 2004a, 2007; Chatterjee et al. 2007). In all cases, the body and wing drag coefficients were computed as functions of the Reynolds number.

Evolutionary Stages of Avian Flight

A sweeping adaptation like flight must have evolved in many stages, over many generations, with each stage of the evolving wing being functional and of adaptive value, setting the stage for the next adaptation (Bock 1985). Phylogeny, paleoecology, aerodynamics, and fossil evidence offer critical insights with which we can retrace the likely sequence of events for the evolution of flight of small feathered coelurosaurs within an arboreal context of progression from climbing to jumping to parachuting to biplane gliding to monoplane gliding, soaring, flapping to complex maneuvering flight (fig. 12.15).

Climbing and Arboreal Leaping

Small coelurosaurs, such as *Sinosauropteryx* (Chen et al. 1998), were agile, lightly built animals that climbed tree trunks quadrupedally (fig. 12.13D) and leaped from branch to branch bipedally as an escape strategy or to reach adjacent trees (fig. 12.16A). Such behavior established the animal's practice of taking to the air temporarily. When nearing a landing place, the forelimbs were outstretched for balance or to grab a branch; they would have conferred enhanced stability and body control.

Simple, hair-like filaments covering the body of *Sinosauropteryx* may have been precursors to feathers, providing insulation in the cooler microclimates of trees. These insulating protofeathers may have reduced loss of body heat and had initial aerodynamic effects. The coat of protofeathers conferred smooth and streamlined body contours on *Sinosauropteryx*, reduced frictional drag on the animal as it leaped among the tree branches, and provided additional protection during any accidental fall. These downy feathers also provided bright body color and could be used for sexual selection and species recognition.

The encephalization quotient of *Sinosauropteryx* at this stage as extrapolated from basal coelurosaurs was 0.25 (Chatterjee 1997). We calculated the leaping trajectory of *Sinosauropteryx* from a perch at 3 meters/second from an initial height of 7 meters; also shown (fig. 12.16A) for comparison is the theoretical trajectory in a vacuum, indicating that for an animal of this size with no wings, aerodynamic forces have little effect on its jumping performance. *Sinosauropteryx* could not slow its speed during a fall. Speed rapidly increased to 6 meters/second after falling from a height of 2 meters, and to 10 meters/second after about a 5-meter drop—probably too high for a safe landing unless the landing surface were compliant, such as a branch or soft, plant-covered ground (Templin 2000). The animal could probably jump from a height of 2 meters onto a hard substrate without injury (Chatterjee and Templin 2004a).

Parachuting

For arboreal coelurosaurs, the first stage of flight evolution was parachuting, when they jumped from a perch and retarded their fall with extended wings without injury. These leaping coelurosaurs might have used outstretched forelimbs and tails to maximize drag and slow descent, softening the impact of landing in much the same way as extant sugar gliders and some squirrels. Some recent tree frogs have been shown to be parachuters. In a fall with the descendant angle > 45°, they launch themselves with a jump, hold their limbs out to the side, and control their orientation so that their flat ventral surface acts as an airbrake for slowing the fall. Additionally, some parachuting frogs spread their webbed feet to act as a flight surface. The ability of protobirds to leap from a great height without injury would have been an important adaptation in the early evolution of flight. Eventually, stiff and collapsible flight surfaces may have evolved in the forelimbs and tails in archaic birds associated with the development of contour feathers. In *Caudipteryx*, *Protarchaeopteryx*, and *Sinornithosaurus* (fig. 12.16B), there is evidence of contour feathers on the remiges and retrices, and down-like feathers on the body (Ji et al. 1998; Xu et al. 2001). Although these contour feathers are long, vaned, and barbed, they are symmetric, indicating these animals probably could not fly or glide effectively (Feduccia and Tordroff 1979), their protowings and feathers being too small to generate enough lift for flight. Our study suggests *Caudipteryx*, *Protarchaeopteryx*, and *Sinornithosaurus* may have had a high wing loading and low aspect ratio. Their small protowings most probably evolved as a safety device for arboreal maneuvering to increase drag and reduce the impact of a fall.

We have computed the parachuting trajectories of *Caudipteryx, Protarchaeopteryx*, and *Sinornithosaurus* with narrow wings using the ANFLTSIM program (Templin 2000). Because the separate trajectories of all three genera were essentially the same, a single curve is presented in figure 12.16B; it displays speed versus height-loss, with the theoretical curve shown for a trajectory in a vacuum (under the same initial conditions). The difference between it and the actual curve reflects aerodynamic forces. Comparison of the two curves shows that even small wings may have a significant effect in "saving" falling animals of this size. The terminal velocity in this case is approximately 11 meters/second, and is 2 meters/second less after a fall of 7 meters from a perch (Chatterjee and Templin 2004b). In our previous study (Chatterjee and Templin 2004a), we calculated the gliding performance of *Sinornithosaurus* (Xu et al. 1999b) assuming that it had a "more modern" wing size, and found that it was capable of phugoid gliding. Downy feathers covered the body of *Sinornithosaurus*, but contour feathers in the hands and tail were not preserved

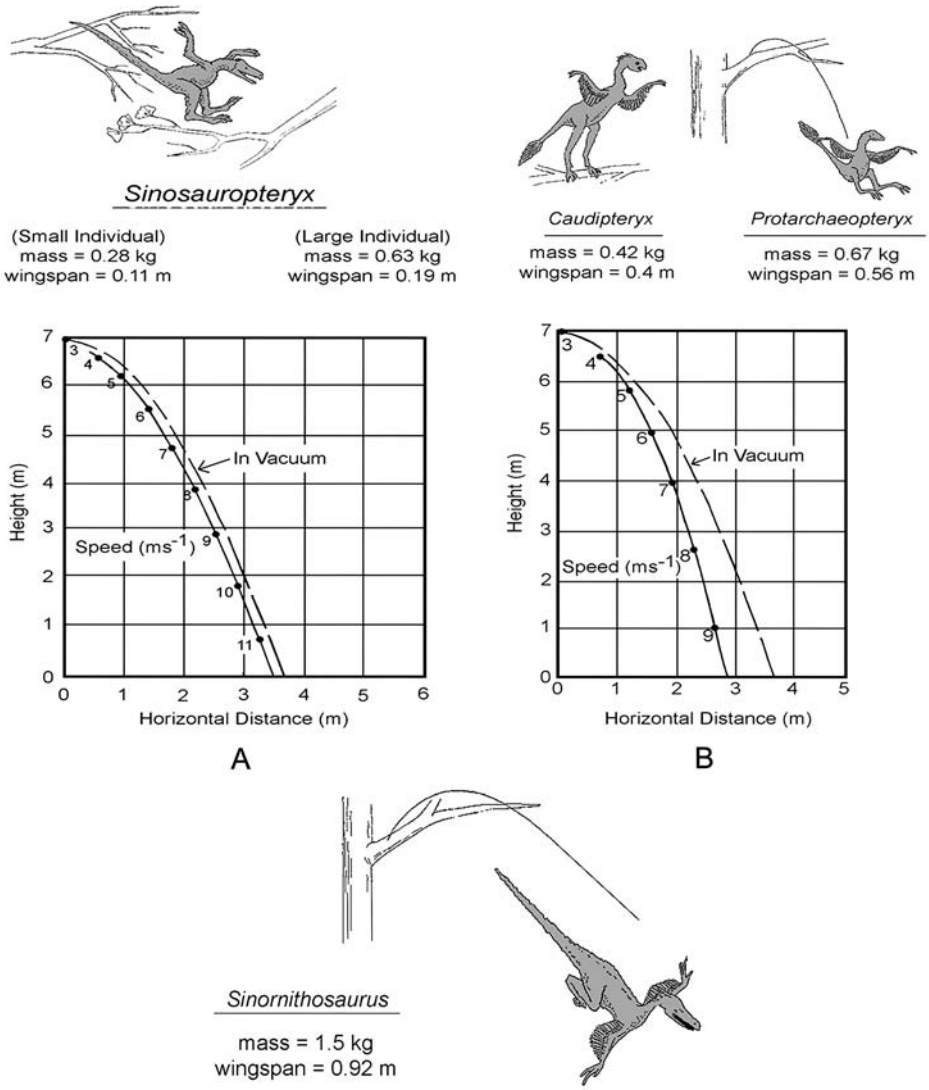


Figure 12.16. A, the leaping trajectory of *Sinosauropteryx*—without proper wing aerodynamics, forces had little effect on its jumping performance. The animal is viewed as leaping from branch to branch to achieve balance while steadying its wings. It could jump from a height of 2 meters onto hard ground without injury (after Chatterjee and Templin 2004a). B, the parachuting trajectory of *Caudipteryx*, *Protarchaeopteryx*, and *Sinornithosaurus* from a perch (a single curve is shown for *Caudipteryx* and *Protarchaeopteryx* because their trajectories are essentially the same). With the development of narrow incipient wings, these animals could have parachuted and retarded their fall from a height (after Chatterjee and Templin 2012).

in the fossil. Because *Sinornithosaurus* is more derived than *Caudipteryx* or *Protarchaeopteryx* and has a relatively long wingspan, we assume that it had acquired a gliding surface. The recent discovery of additional material from a juvenile specimen suggests that *Sinornithosaurus* developed two types of branching structures: filaments joined in a basal tuft and a feather with a central rachis and serially fused barbs forming a pair of symmetrical vanes (Xu et al. 2001). However, it lacked sturdy contour feathers with sufficient structural integrity to form an effective gliding surface. We recalculated the flight performance of *Sinosauropteryx* (fig. 12.16B) with its narrow wings and found that it could parachute but not glide. Possibly *Sinornithosaurus* was reverting to flightlessness as had some other feathered maniraptorans; this is reflected in its fluffy wing feathers.

Biplane Gliding

The second stage in the evolution of flight was biplane gliding, documented by several members of tetrapterygids, wherein the pull of gravity provides the force required for forward airborne movement that preceded powered flight. Gliding is a simpler and cheaper way of flying than flapping the wings. Most seabirds, with long and narrow wings, are primarily gliders. Gliding evolved independently in many groups of vertebrates, including lizards, colugo, phalangers, anomalurid rodents, pterosaurs, and birds (descendant angle < 45°). Gliders stretch their motionless wings to form one lifting surface and passively descend through the air in response to gravity. An arboreal theropod launched from on high was deflected from the line of fall and its horizontal travel increased.

The next stage was powered biplane gliding where the pull of gravity and asymmetric primary wings in both hands and feet would generate thrust and extend airborne time. Of all the feathered coelurosaurs from China, *Microraptor* is probably the most unusual in development of a biplane wing planform, possibly a precursor to the monoplane design of *Archaeopteryx* and later birds (Xu et al. 2003; Chatterjee and Templin 2007, 2012). Refinements in its flight apparatus seem to reflect the gliding capacity of *Microraptor* (Xu et al. 2003). Its shoulder girdle is similar to that of *Archaeopteryx*: the glenoid facing laterally, allowing gentle extension of the wing; a scapulocoracoid with ends oriented at an acute angle to each other; a single enlarged sternum for attachment of flight muscles; ossified sternal ribs and well-developed uncinate processes for resisting compressive forces on the thoracic cavity imposed during downstroke; development of the swivel wrist joint for an automatic wing-folding mechanism; a strongly bowed outer metacarpal; a flattened digit for attachment of the primaries; and elongated asymmetric vanes in the flight feathers.

The two sets of wings of *Microraptor*, one above the other, may have functioned much like those of a staggered biplane from the side, where the forewing forms the dorsal wing and the metatarsal wing forms the ventral one (fig. 12.17A). The distribution of feathers across the dorsal wings of the biplane resemble those on the wings of *Archaeopteryx* and *Jeholornis*, but the presence of flight feathers on the feet, forming ventral wings, is the most unusual feature. *Microraptor*'s set of long asymmetric feathers with hooked barbs on the forelimbs and hindlimbs (fig. 12.17B, C) was an innovation, a prelude to a monoplane design. The leading edge of each long primary feather in both hands and legs was asymmetric, narrower than the trailing edge, helping to generate lift and drag. The hooked, interlocking barbs gave strength and flexibility to the feather and prevented air from passing through it during flight. Asymmetric feathers are essential for flight (Feduccia and Tordroff 1979); their presence on the metatarsals would have made walking or running on the ground nearly impossible.

Gliding performance can be measured by a polar curve constructed by plotting horizontal speed against sinking speed—determined primarily by wing loading so that lighter, larger gliders descend more slowly than do smaller, heavier ones. We used the ANFLTSIM program to calculate the possible gliding performance of *Microraptor* compared with that of a seabird (frigatebird) and a pterosaur of similar size (*Nyctosaurus*) (fig. 12.17D). Results show that *Microraptor* was probably a moderately efficient glider compared with the long-wing-span frigatebird or the Cretaceous pterodactyloid *Nyctosaurus*. Predicted glide paths of *Microraptor* from a perch suggest that its biplane wings were adapted for undulatory phugoid gliding between trees (fig. 12.17E). Evolution of the ventral wing, as observed in *Microraptor*, may be an adaptation for increasing gliding efficiency. The aerodynamic efficiency of modern biplane aircraft is inferior to that of monoplanes because of the drag of the supporting struts and wires that are required to stiffen the lightweight biplane wing assemblies. Structural scaling rules show that stresses decrease steadily as the size is reduced, so that the wings of *Microraptor* would not have required external bracing. It was demonstrated more than seventy years ago (Prandtl and Tietjens 1934) that the total induced drag of a cantilevered plane is theoretically smaller than that of a monoplane of the same span and with the

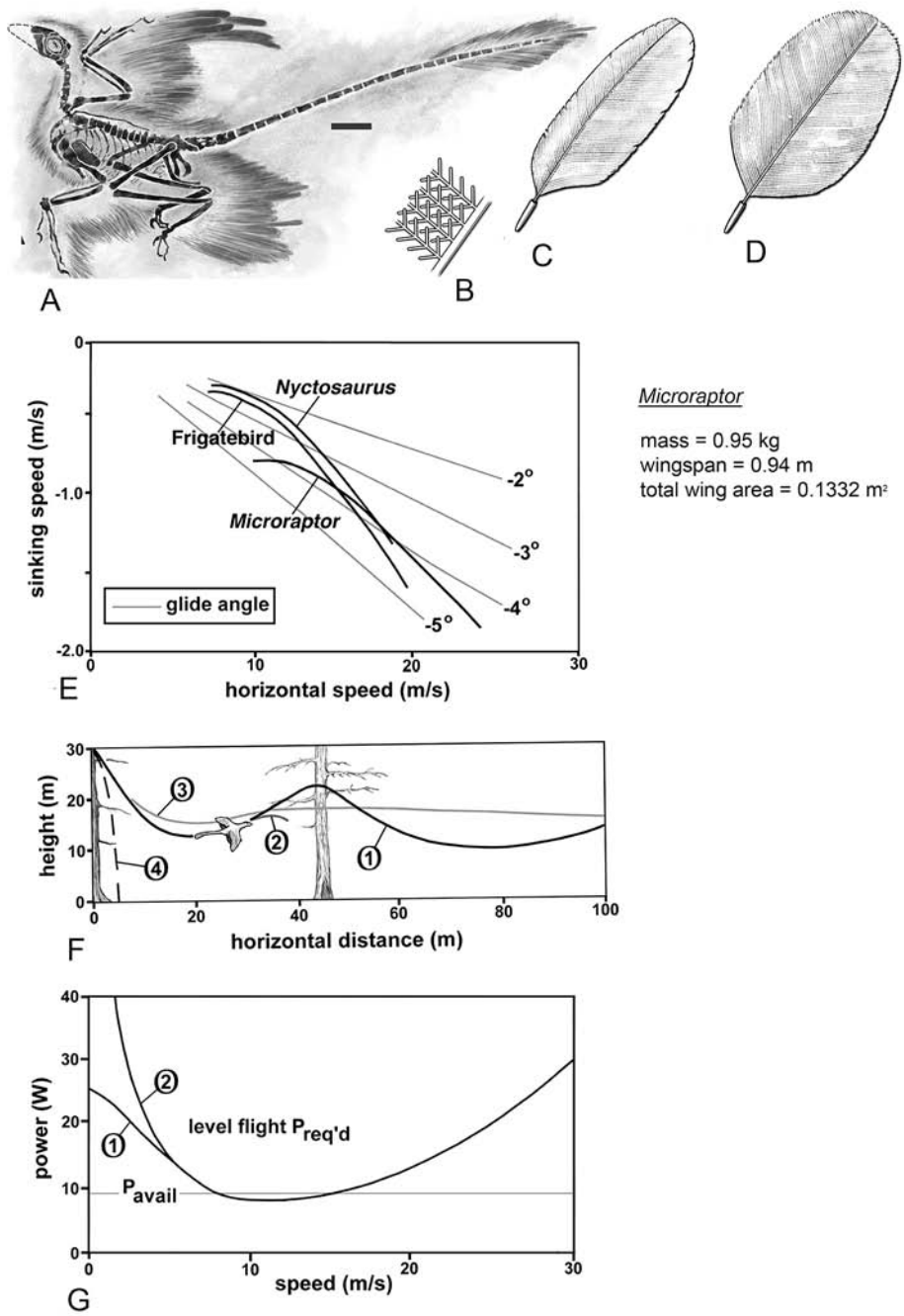


Figure 12.17. A, holotype of *Microraptor gui* showing two sets of wings. B and C, interlocking barbules of the long, asymmetric feathers of the hand and foot of *Microraptor.* D, symmetric feathers of the wings and hindlimbs of other coelurosaurs. Graphs of flight potential: E, glide polars of *Microraptor* compared with a seabird (frigatebird, M = 1.5 kilograms) and a pterosaur (*Nyctosaurus*, M = 1.86 kilograms); the polar curve shows that *Microraptor* was an efficient glider. F, glide paths of *Microraptor* from a perch; curve 1 shows phugoid gliding; curve 2, a final rapid pitchup with high drag; curve 3, a gliding path with the pitch damper on; curve 4, a parachuting trajectory. G, power curves (steady level flight) for *Microraptor*; the horizontal line represents the estimated maximum continuous power available; two curves are shown for level flight: the U-shaped curve is the power required for level flight, whereas the horizontal curve represents the power available. Because they converge at speeds greater than 6 meters/second, an incipient level flight was possible for *Microraptor* (after Chatterjee and Templin 2007).

same total lift. For the *Microraptor* biplane configuration, the improvement is a maximum lift-to-drag ratio, or glide angle, which would have been small (perhaps about 5%) but not negligible.

With the ANFLTPWR program, we calculated the possible steady level flight capacity of *Microraptor* (fig. 12.17F). Because the two curves, power required and power available, nearly coincide at flight speeds of 9 to 15 meters/second, limited steady level flight may have been theoretically possible. Therefore, *Microraptor* may have been primarily a glider that had begun to acquire a limited amount of flapping flight.

Phylogenetically, *Microraptor* is currently considered to belong to the Paraves (Sereno 1997), a group that also includes troodontids, dromaeosaurs, and Avialae. In my phylogeny I have grouped *Microraptor* within tetrapterygids, a sister group of avialans (fig. 12.15). Basal members of all three groups had long contour feathers on their lower legs and feet. Surprisingly, *Archaeopteryx* had long contour feathers on the hindlimbs, especially in the tibial region, as seen in the Berlin specimen. It apparently lacked metatarsal feathers or ventral wings; this was compensated by development of large forewings and long frond-like asymmetric retrices to provide additional lift surfaces. We were intrigued by the biomechanical functions of the tibial feathers in several Chinese maniraptorans, *Archaeopteryx*, and modern raptors (fig. 12.18A) and concluded that these feathers conferred streamlining and stretching effects on the cylindrical tibia to reduce drag during flight (Chatterjee and Templin 2007). Like modern raptors, these maniraptorans probably kept their hindlimbs in a Z-configuration during their preparation for aerial attack and, while carrying prey, dangling their tibiae in a vertical plane. The leg feathers kept their prey-catching structures streamlined during flight.

The biplane wing planform has been identified in several Chinese tetrapterygids including *Microraptor*, *Anchiornis* (Hu et al. 2009), *Xiaotingia*, as well as the basal pygostylian *Sapeornis* (Zheng et al. 2013) that had long contour feathers on the lower legs and feet (fig. 12.18A). These averaptorans retained full complements of stiff, aerodynamic contour feathers covering the entire leg—including the femur, tibia, and metatarsus, suggesting that biplane wings first arose in paravians and continued on in the early birds and finally receded to monoplane wings. In *Microraptor*, the metatarsal feathers are proportionately large with highly asymmetrical vanes, whereas in *Pedopenna*, *Anchiornis*, and *Sapeornis* they are proportionately smaller and have nearly symmetrical vanes. Thus the two sets of wings in *Pedopenna*, *Anchiornis* and *Sapeornis* probably indicate its biplane wing design, but the small and symmetric nature of the metatarsus feathers indicate that these animals were on their way to disposing of the ventral wings as the forewings became larger to compensate for the reduced flight surface of the ventral wings. Biplane wing configuration was a stable design for gliding as it provided additional lifting surface, but poorly designed for maneuvering flight. Flight performance was gradually enhanced with the increase of the forewing area and the gradual decrease of the hindwings, which were cumbersome during aerial turns and terrestrial locomotion. Zheng et al. (2013) noted a distal to proximal reduction pattern of leg feathers in the early evolution of birds. Pygostylians such as *Sapeornis* had full complements of hindwings including metatarsal feathers; enantiornithine birds such as *Cathayornis* lost the metatarsal feathers but retained tibial feathers, whereas in ornithuromorph birds, both metatarsal and tibial feathers were lost and were replaced by scaled feet (fig. 12.18).

The unusual biplane wing configuration of *Microraptor* and several other Chinese averaptorans raises an interesting evolutionary possibility: Did avian flight go through a *Microraptor*-like biplane stage in development of a monoplane configuration, like that of *Jeholornis* and *Archaeopteryx*? The phylogeny of the Maniraptora indicates a gradual shift in the evolution of flight from biplane wing planform to a monoplane wing, as paralleled in the evolution of aircraft design (fig. 12.18B, C). The Wright brothers took to the skies in 1903 with their biplane *Flyer* with two pairs of parallel wings, but by 1909, the faster monoplane design by Bleriot, with just two wings, dominated aviation in the First World War. Dramatic fossils from China suggest that early birds went through a similar evolution from biplane to monoplane configuration as

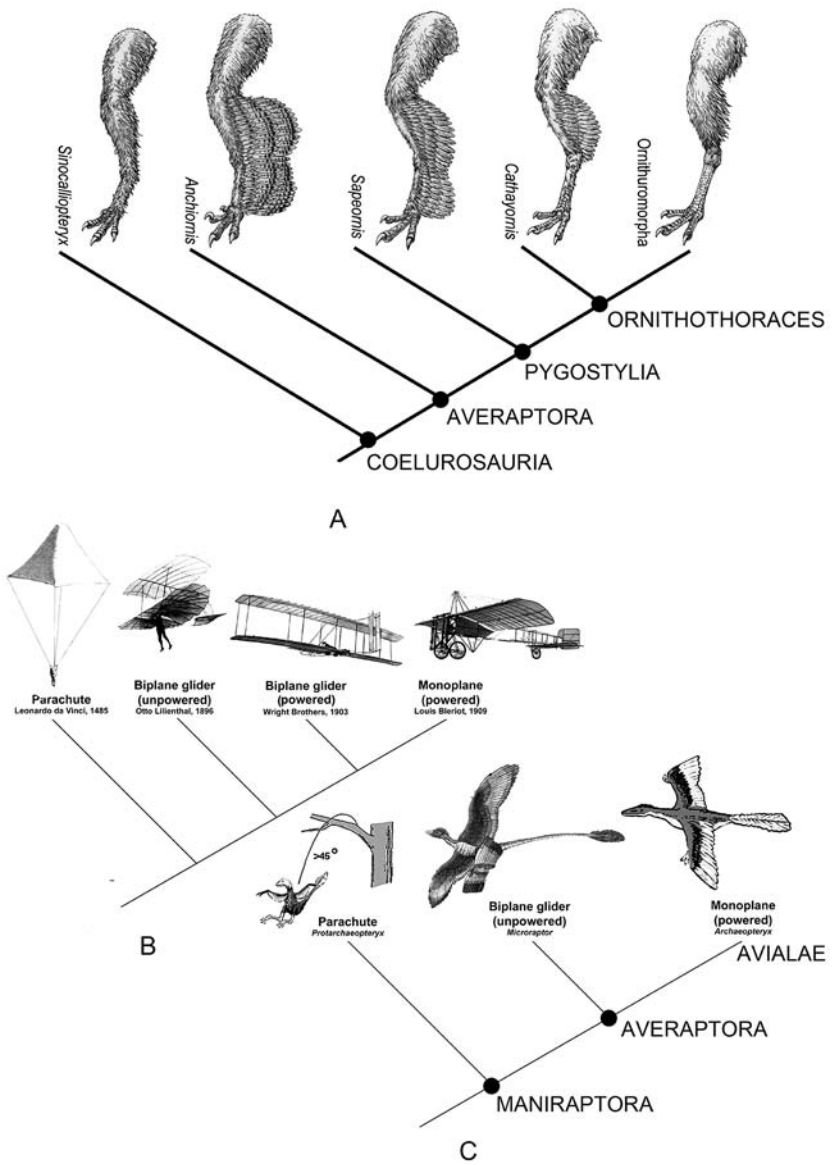


Figure 12.18. Evolution of monoplane wings in birds from a biplane structure. A, coelurosaurian theropods showing distribution of the leg feathers in selected taxa; four major stages in the evolution of integumentary structures on the hindlimb are represented by the coelurosaurian *Sinocalliopteryx* (short filamentous covering of the legs, including the feet); the averaptorans such as *Anchiornis* and *Microraptor* with a biplane wing planform (long contour feathers on the legs, including the tibia and feet, forming a wing-like structure); although hindwings made of metatarsal feathers are lost in basal avialans such as *Archaeopteryx* and *Jeholornis* with the evolution of monoplane design, a biplane wing planform is retained in the basal pygostylians such as *Sapeornis*; in an enatiornithine bird such as *Cathayornis*, large tibial feathers are retained as in modern raptors; and in ornithuromorphs, small femoral and tibial feathers are present but feet became featherless (modified from Zheng et al. 2013). B–C, the early evolution of aircraft, from parachute to biplane glider to monoplane, shows an uncanny convergence with the early evolution of avian flight as documented by fossil evidence. Man learned to fly independently by progressing through stages analogous to those of the protobirds millions of years earlier, with no prior knowledge. He started with the parachute, then moved on to short glides, which gradually led to longer glides with powered biplane wings, and then to the monoplane, refined over the years. Most early aircrafts were biplanes, but by the 1930s, the faster monoplane design, with just two wings, dominated aviation. From this early monoplane stage, aeronautical technology diverged very rapidly from the avian model. Dramatic feathered dinosaur fossils from China suggest that early averaptorans were biplanes, starting off with wings on both arms and legs and only later adopting the arms-only, monoplane configuration in early avialans such as *Archaeopteryx* and *Jeholornis*, similar to the pattern of aircraft evolution. Like modern aircrafts, biplanes coexisted with monoplanes as shown by the biplane wing configuration of the more derived pygostylian *Sapeornis* (top cladogram).

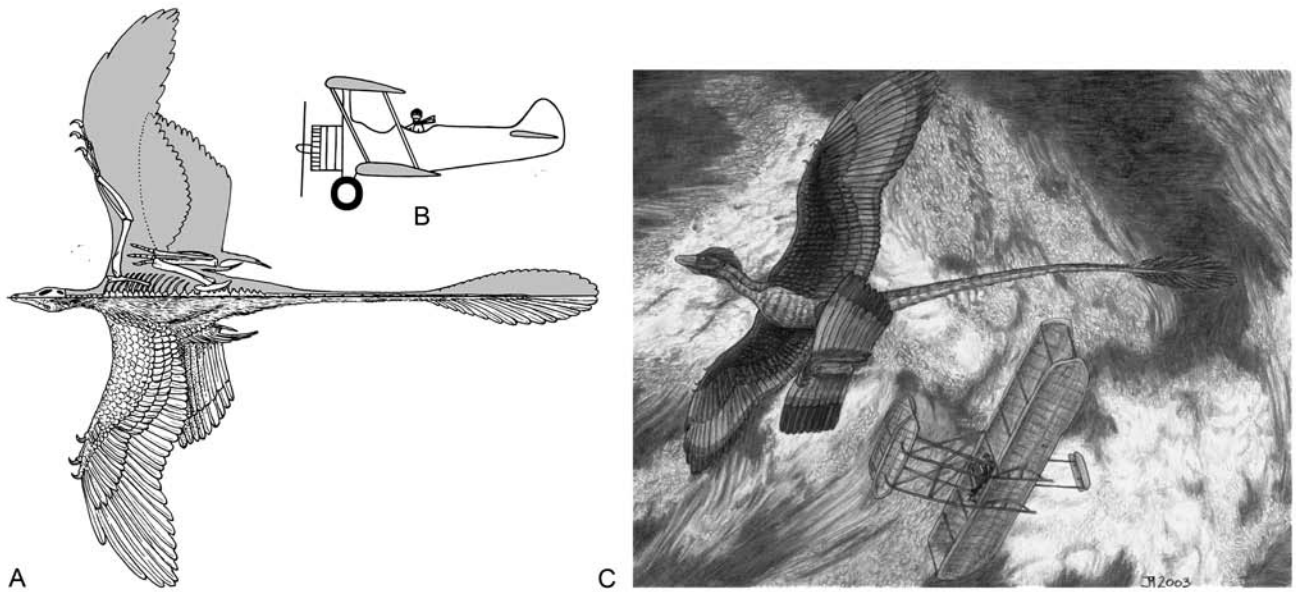


Figure 12.19. A, life reconstruction of *Microraptor gui* in dorsal view showing the morphology and distribution of hindlimb feathers (*left*) with biplane wing planform and orientation of the hindlimb (*right*) during gliding. B, a typical staggered biplane (Stearman 75) for comparison with *Microraptor*; in biplane aircraft of the 1920s, there was additional drag of wires, struts, and so on between the two wings, which eventually made the biplane obsolete except for a niche application; such drag-induced structures were absent in *Microraptor*. C, reconstruction of *Microraptor* showing its biplane wing planform compared to the Wright brothers' 1903 *Flyer* (modified from Chatterjee and Templin 2007, 2012).

flight improved (figs. 12.18, 12.19). It seems likely that *Microraptor* invented the biplane 125 million years before the Wrights' 1903 *Flyer*!

Monoplane Gliding

The third stage was the beginning of monoplane gliding flight, documented by basal avialans such as *Archaeopteryx* and *Jeholornis*. They still retained a long bony tail with frond-like retrices for stability and lift, as well as developing fully formed wings with a long span and asymmetric flight feathers on the hands and tail to provide greater lift and a larger flight surface. The forewings became larger than *Microraptor*'s, but the foot feathers were lost on the hindlimbs forming, in essence, a gliding monoplane. The long and asymmetric flight feathers on the hands and long bony tail provided large lift and flight surfaces, formed a novel allegiance to the locomotor module, and offered stability. Since our knowledge of the flight dynamics of *Jeholornis* is still sketchy, I use *Archaeopteryx* as a substitute for *Jeholornis* in representing the monoplane gliding stage. *Archaeopteryx* shows long contour feathers on the hindlimb, especially in the tibial region; it apparently lacked metatarsus feathers, which was compensated for with larger forewings and long asymmetric tail feathers for additional lifting surfaces. The arrangement of the flight feathers suggests some degree of powered flight ability in *Archaeopteryx*, but the wings lack the alula on the freely moving first digit used by modern birds when flying at low speed or when landing. The lack of an alula may have been traded for climbing claws, another piece of evidence consistent with the arboreal theory. During an early stage of active flight, the capacity of these birds to become fully airborne increased. It is easy to envisage, from the example of *Archaeopteryx* and *Jeholornis*, how flapping flight could have developed from a gliding animal that was already adapted for controlling wing movement during takeoff from a perch and landing (Norberg 1990). Flapping flight entails a downstroke, when the wing is brought downward and forward to provide thrust, and an upstroke that prepares

the wing for the subsequent downstroke. Powered flight requires much more energy than gliding. Energy comes from the flight muscles moving the wings up and down to keep the animal airborne against the pull of gravity.

The flight apparatus of *Archaeopteryx* remained virtually unchanged from that of its maniraptoran predecessors. For example, it lacked the bony sternum that houses the flight muscles. The pectoralis and supracoracoideus muscles of birds are the principal depressor and elevator of the wing, respectively. However, *Archaeopteryx* lacked the supracoracoideus pulley, the primary elevator of the wing required to execute the upstroke, a condition necessary for ground takeoff and active-flapping flight (Poore et al. 1997). Its glenoid faces laterally instead of dorsolaterally, the position seen in modern birds, indicating limited elevation of the wing above the horizontal position. It could raise its wings with its deltoideus muscles to some extent, slightly above the horizontal position, but not enough to generate a powerful thrust in the following downstroke (Jenkins 1993). Because the wrist of *Archaeopteryx* lacks the interlockings and fusions of the carpus seen in modern birds, it would have been unable to stop the manus from hyperpronating during a downstroke of sufficient force to propel it forward (Vasquez 1992). Some (e.g., Bock 1986; Ostrom 1976a) consider that *Archaeopteryx* was at best a glider, or more probably a poor flier.

Several features in the brain and inner ear indicate clearly that *Archaeopteryx* was a flying bird. It shows the bird-like brain organization with development of large, separated optic lobes for keen sight and enlargement of the cerebellum for balance and control (fig. 12.20A). Its brain had developed typical avian architecture and was considerably enlarged from that of its nonflying precursors, with an estimated EQ of 0.34 (Chatterjee 1997). Recent computed tomographic x-ray scanning images suggest that *Archaeopteryx* had developed the movement and balance control required for powered flight and not just gliding; this is evident from the topography of the inner ear with large semicircular canals with a vestibular apparatus (Alonso et al. 2004). The brain is relatively bigger than those of nonflying coelurosaurs. Our flight analysis reflects the neural specialization of *Archaeopteryx* and

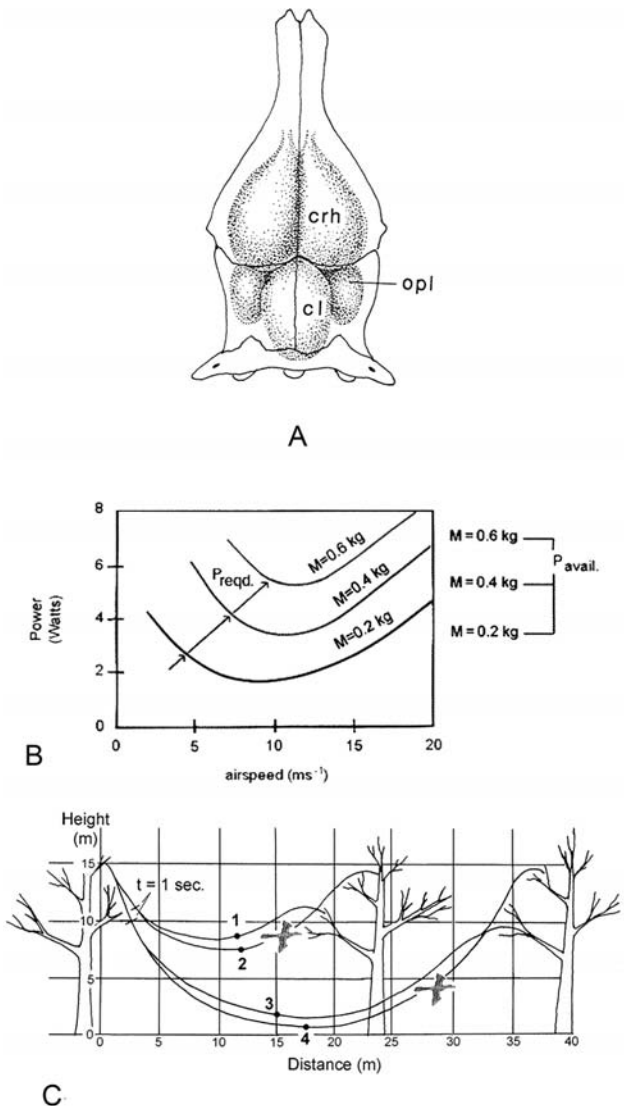


Figure 12.20. A, morphology of the brain of *Archaeopteryx* in dorsal view showing the three important components arranged in avian fashion: large cerebral hemispheres (crh), cerebellum (cl), and optic lobes (opl). B, flight performances of three individuals of *Archaeopteryx* with different masses and body sizes: Eichstätt specimen (M = 200 grams), London specimen (M = 400 grams), and Solnhofen specimen (M = 600 grams). Power curves (steady level flight) are depicted for the three specimens of *Archaeopteryx*. In all three cases, the power-available horizontal curves (*right*) intersect the U-shaped power-required curves, generated by the ANFLTPWR computer program indicating that *Archaeopteryx* achieved powered flight. C, phugoid gliding paths of *Archaeopteryx* from a height of 15 meters with a launch speed of 2 meters/second (horizontal). Phugoid gliding allowed *Archaeopteryx* to make short flights between trees without muscular effort (after Chatterjee and Templin 2003).

suggests that it had acquired an initial stage of powered flight (Chatterjee and Templin 2003, 2004a).

To analyze the steady level flight of *Archaeopteryx*, we selected three groups of individuals of different size (mass = 0.2, 0.4, and 0.6 kilogram), representing the Eichstätt, London, and Berlin specimens, respectively. For any flying animal, fixed-wing aircraft, or helicopter, the plot of power required for level flight against airspeed is a U-shaped curve, higher at both ends than at the middle. Using the ANFLTPWR program, we generated three power curves for *Archaeopteryx*, representing the three size groups—each U-shaped curve is the power required for steady level flight and the corresponding horizontal line on the right side of the curve is the estimated maximum steady power available (fig. 12.20B). Because the predicted available power exceeds the minimum power at each size, *Archaeopteryx* appears to have been capable of initial stages of powered flight. However, the narrow primary rachises of *Archaeopteryx* would have curtailed its flapping ability (Nudds and Dyke 2010).

Assuming that *Archaeopteryx* was a tree-dweller, as is apparent from its climbing wings and reversed hallux and the highly recurved pedal claws for perching on branches (Feduccia 1993), we calculated the gliding performance of the above three specimens of *Archaeopteryx* launching from a height of 15 meters. We used the ANFLTSIM program to generate glide polar curves (fig. 12.20C). It appears that, like *Microraptor*, *Archaeopteryx* was probably capable of phugoid gliding between trees, possibly as an energy conservation strategy. We also calculated the relative energy costs between a ground takeoff and an arboreal takeoff for *Archaeopteryx*, using these three individuals. In all cases, considering the energy required, an arboreal takeoff appears to have been more efficient and cost effective than a takeoff from the ground (Chatterjee and Templin 2004b). Most likely *Archaeopteryx* was an obligatory monoplane glider and had developed short flights between trees, utilizing a novel method of phugoid gliding without expending much energy. It would launch from a perch to initiate gliding. The animal would lose height at first, and then sweep up with a large-amplitude undulation to initiate phugoid gliding for traveling from tree to tree. Many modern birds such as crows use a similar strategy to move from tree to tree.

Another long-tailed primitive bird in the Jehol biota, *Jeholornis*, is similar to *Archaeopteryx* in its gross anatomy, but its tail is much longer than that of *Archaeopteryx* and its tail feathers are shaped like distal fans, as seen in the dromaeosaurs (Zhou and Zhang 2003). The hallux is reversed and the claws, large and curved, indicate arboreal adaptation. Compared with *Archaeopteryx*, *Jeholornis* shows some advancement in the flight apparatus: the glenoid faces dorsolaterally; the coracoid is strut-like; the sternum is ossified with lateral trabeculae; there is development of the interclavicular sac; the carpometacarpus is fused with a bowed metacarpal III (presumably one on each side); and digit 2 is shortened and more robust, more suitable for attachment of flight feathers. Like *Archaeopteryx*, *Jeholornis* was probably still a monoplane glider with a long bony tail, though more efficient.

Soaring

The fourth stage of flight evolution is represented by soaring flight as documented by pygostylians such as *Confuciusornis*, a beaked and short-tailed bird from the Jehol Group (fig. 6.2) (Hou et al. 1995). Soaring flight is gliding in circles where height is maintained or gained by rising air. Soaring birds take advantage of updraft from wind currents by circling in rising currents of warm air called thermals by banking their wings. Great savings in the cost of flight can be made if the bird can extract energy from the rising air. To see a bird rise in the air and sail on motionless wings into the distance until at last it disappears from sight is a magical experience. As seen in *Archaeopteryx*, a well-designed tail with long, narrow, frond-like retrices is one of the most effective stabilizers; it is an inbuilt and essentially permanent feature. A long bony tail gives a flier passive stability, providing steady flight and avoiding unintentional changes (Alexander 2002). Stability was reduced by transforming the long bony tail into a short tail with few vertebrae and a short pygostyle with caudal vertebrae fused into a single bone supporting the fan of tail feathers and the musculature—as seen in the clade Pygostylia. The pygostyle has an important function in

controlling flight, steering, and braking. With loss of the tail, the pygostylians became unstable but more maneuverable, and could take sharp aerial turns, which would be advantageous for thermal soaring. To stay within a thermal, a bird must be capable of turning fairly tight circles as close as possible around the center.

Several Chinese birds from Jehol Group such as *Zhongornis*, *Sapeornis*, and *Confuciusornis* represent the basal radiation of the Pygostylia (fig. 7.4). *Confuciusornis* is one of the most abundant bird fossils in the Jehol biota—more than one thousand skeletons have been obtained. Several refinements in the flight apparatus in *Confuciusornis* from the *Archaeopteryx*-like body plan are known. The relatively large wings, the arrangement of flight feathers, a robust furcula, a large deltoid crest on the humerus, a large ossified sternum with a subdued keel, and partially fused wrist bones suggest that downstroke had already developed in *Confuciusornis* to generate both lift and thrust, thereby enabling powered flight. Its hand had more flexing ability that helped during upstroke to reduce the wingspan. However, the orientation of the glenoid in the lateral position and the lack of a supracoarcoideus pulley indicate that upstroke was still not perfected in *Confuciusornis*. Takeoff from the level ground would be difficult at this stage because of the absence of the supracoarcoideus pulley and narrow primary rachises, which were not hollow as in living birds (Nudds and Dyke 2010). Most likely *Confuciusornis* was a feeble flapper toward the gliding end of flight, incapable of the vigorous flapping flight of modern birds.

A pygostylian was clearly an arboreal bird, as evidenced by long, curved, and laterally compressed pedal claws and the proportion of pedal phalanges. It would take off from a perch and remain airborne by an alternating sequence of gliding and flapping its wings, called undulating flight. However, pygostylians probably exploited thermals for cross-country riding as they became maneuverable. A canopy of cumulus clouds, which is often formed by rapidly rising warm air at high altitude, is the landmark for locating a thermal. Like modern birds, pygostylians could probably spot cumulus clouds for locating useful thermals (fig. 12.7B). When a pygostylian encountered a thermal, it would sense the lift and spiral around to take advantage of it. It would launch from a perch and would need a little muscle power to get airborne and enter a thermal. Once within a thermal, a pygostylian could fly all day by riding rising currents of thermals. It probably used thermal soaring over vast open expanses of large flat areas while searching for food.

Other than soaring, pygostylians were capable of undulating flight after launching from a perch, which might be a precursor to flapping flight. The animal had to glide to achieve the upstroke position by vertical air resistance. The height lost during gliding was regained in the next downstroke. Many living birds, such as starlings, bee-eaters, swifts, swallows, and fulmars, employ this kind of undulating flight path to save muscular energy (Burton 1990). The partially fused synsacrum, tibiotarsus, and tarsometatarsus in *Confuciusornis* strengthened the landing gear. Moreover, the truncated bony tail and a long pygostyle made *Confuciusornis* less stable during level flight but more agile and maneuverable. It is easy to envisage from the example of *Confuciusornis* how undulating flight could give rise to true powered flight as seen among enantiornithine birds.

Flapping Flight and Ground Takeoff

The fifth stage of flight, flapping flight, was achieved by enantiornithine birds. Enantiornithes were a diverse and dominant clade of Cretaceous birds, known from Spain, China, Argentina, and Mongolia, and occupied various niches. The early forms were small sparrow-sized perching birds, similar in lifestyle to modern songbirds. Smaller sizes reduced wing loading considerably and demanded less aerobic power to fly. No doubt, early enantiornithines were efficient fliers. There is a trend toward increasing body size in Late Cretaceous forms. Some enantiornithines became aquatic, others adapted to the lifestyle of shorebirds, and yet others became secondarily flightless. They exhibit considerable upgrading of the flight apparatus from the pygostylian stage such as a broad sternum, a flexible scapulocoracoid joint with a strut-like coracoid, a spring-like furcula, a wing-folding mechanism, and a short and fused pygostyle. They devel-

oped a primitive triosseal canal entirely confined to the coracoid, allowing for a wide range of upstroke movements. The glenoid faced upward and outward to amplify the range of the wingstroke for flapping flight. They developed an alula that delayed stalling during slow flight during takeoff and landing. Although the sternum was relatively short compared with that of the ornithurine birds, it had a keel for housing the flight muscles. Therefore enantiornithines possessed a more advanced flight apparatus than basal pygostylians, with increased wingspan and powerful flight muscles enabling them to take off from the ground and flap their wings vigorously to become airborne, replacing the need for tree climbing (fig. 8.2). Enantiornithines were strong fliers. They had developed powered flight with complex wing movements. However, flight muscles were still not very powerful as is evident from the weak keel of the sternum. Most likely, enantiornithine birds flew low and slowly. Moreover, they retained many primitive features in the pelvis and hindlimbs, indicating their landing gear was not perfected at this stage.

In basal ornithuromorphs, we see further upgrading of the flight apparatus with the development of a propatagium, a shoulder joint with a modern suparcoarcoideus pulley, a keeled sternum, powerful and elongated wings, a humerus with a spherical head for wide excursion of wingbeats, a highly fused metacarpus, digital reduction and loss of terminal claws, and a highly reduced and plowshare-shaped pygostyle for the attachment of fan-like tail feathers as seen in modern birds (fig. 9.3). With the development of a propatagium, Ornithothoraces could change the camber of the wing when needed. However, the pelvic girdle and hindlimbs still retained primitive features, indicating that complex landing maneuvers were not yet perfected.

Maneuvering Flight

The final stage in the evolution of flight is the development of highly acrobatic maneuvering flight, exhibited by the ornithurine birds, such as *Ichthyornis* from the Upper Cretaceous of Kansas. *Ichthyornis* possessed sophisticated flight skills to take off and land, as well as to control flight. It was capable of performing different styles of flight, ranging from fast flight to slow flight to hovering, gliding, and soaring, like modern birds (fig. 12.21). They acquired maneuvering flight and could intentionally change direction of flight, both vertically and horizontally, and were able to turn sharply to exploit thermals. Moreover, they perfected landing skills that require exquisitely fine control of vertical direction and speed. In this group although the skull is primitive with retention of teeth on the maxilla and dentary, the flight apparatus is modern in appearance. The sternum was enlarged with development of a strong keel for attachment of the flight muscles (fig. 9.6B). The wings were very long and powerful, the glenoid faced dorsolaterally allowing large excursions of the dorsal and ventral movements of the wings, and the development of an alula prevented stalling during takeoff and landing. The ribcage was strengthened by ossification of the uncinate process. The pelvis and hindlimbs were highly modified like those of modern birds by a large degree of bone fusion at the joints. Ground takeoff and landing were also perfected at this stage with development of the synsacrum, the fused tibiotarsus, and the fused tarsometatarsus (Chatterjee 1997). The wrist was modified in such a fashion that the manus could be locked in place during the downstroke (Vasquez 1992). As a result, various subtle and complex flight-related movements of the wings could be performed. That it had achieved long-distance maneuvering flight may have contributed to the wide distribution of *Ichthyornis*.

Ichthyornis was a heavy-billed carinate about the size of a gull, with a body mass of about 230 grams and an estimated wingspan of 90 centimeters. We have used empirical methods to calculate the maximum available power from the body mass of *Ichthyornis*. Using the ANFLTPWR program, we have generated the power of *Ichthyornis*, where the U-shaped curve is the power required for steady level flight (fig. 12.21). In the power curve, the horizontal line represents the estimated maximum continuous power available (3.8 watts), assuming flight muscle mass comparable to the average percent of living seabirds; the U-shaped curve represents the power required for steady level flight (1.2 watts). It appears from the power curve that for *Ichthyornis*, the available power is more than three times the power required for steady level flight. Because there is

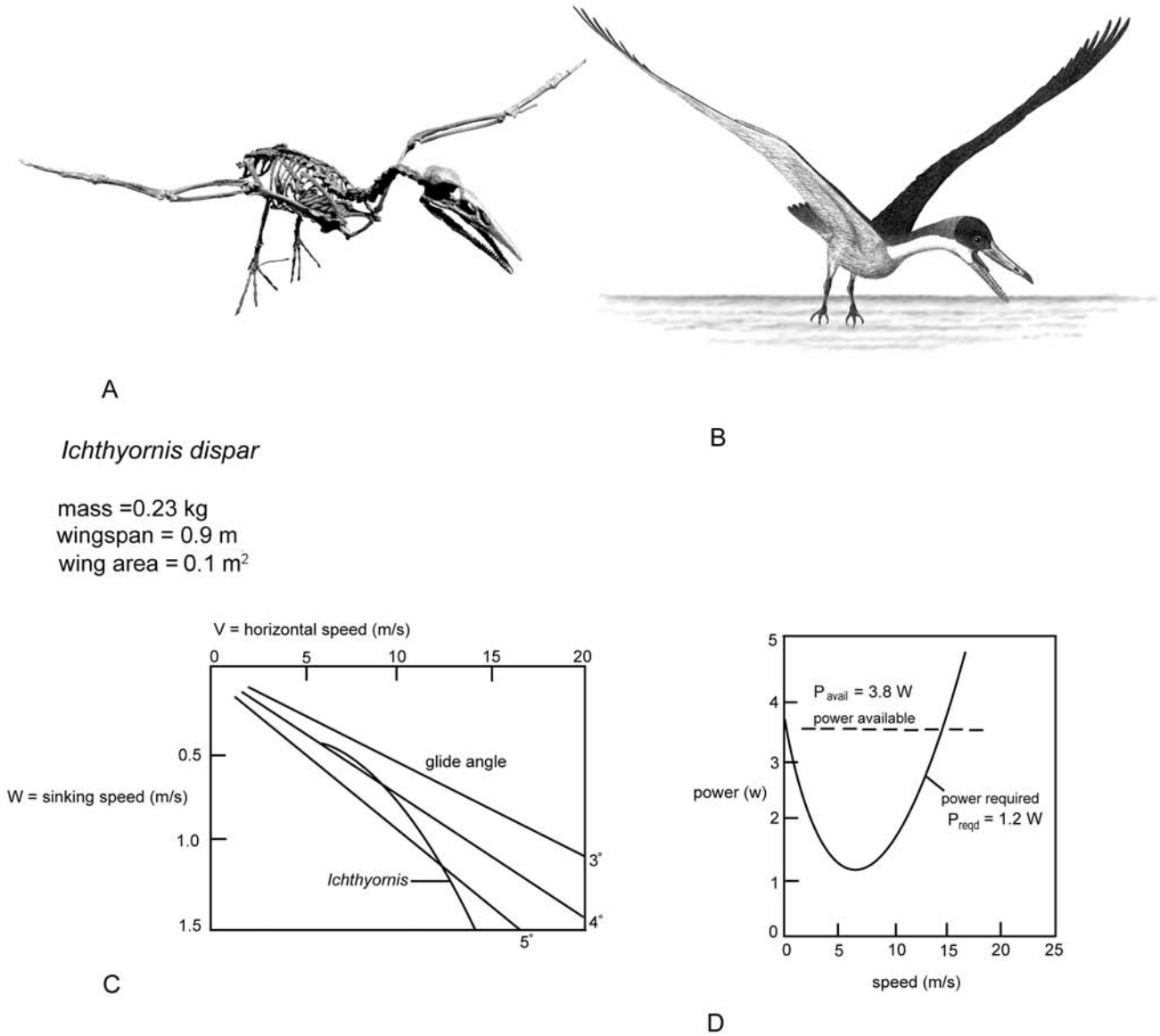


Figure 12.21. A, skeletal reconstruction of *Ichthyornis* during landing at the Natural History Museum of Kansas University (courtesy of David Burnham); *Ichthyornis* developed modern flight apparatus with a keeled sternum that allowed this seabird to perform complex maneuvering skills. B, life reconstruction of *Ichthyornis* from the Late Cretaceous of Kansas. C, polar curve of *Ichthyornis* showing excellent soaring capability; most likely, *Ichthyornis* adopted hover feeding near the surface of the water to catch fish. With long and narrow high-aspect ratio wings (8.2), *Ichthyornis* soared over the Western Interior Seaway for a long distance, extracting energy from the gradient in the lower portion of the atmosphere. D, the U-shaped power curve generated by the ANFLTPWR computer program indicates that *Ichthyornis* was capable of hovering as well as continuous flapping flight because the available power exceeds the required power at zero speed.

wide gap between these two power curves that intersect, *Ichthyornis* had enough power to be capable of flapping flight, permitting high maneuverability. Like most small fliers, *Ichthyornis* had excess power available above that required for steady flight over a fairly wide speed range, which would have given the animal good agility. The most efficient cruising speed occurs at about 8 meters/second (or 29 kilometers/hour). The most common style of flight adopted by *Ichthyornis* was steady level flight. Maneuvering flight while maintaining speed requires extra power

to overcome the increased drag in level banked turns or rapid pull-ups. The small size, large flight muscles, short stumpy pygostyle, complex wrist joints, and rigid hands indicate that *Ichthyornis* was capable of hovering and flapping flight and could take off from the ground by flapping its wings with its excess available power. For *Ichthyornis*, the power available from flight muscles would far exceed the required power at zero speed and it was evidently capable of hovering flight. The narrow, swept-back wings with a flat camber and the large flight muscles suggest that *Ichthyornis* was adapted for high-speed flight. Like modern gulls, *Ichthyornis* could hover just over the water surface for few seconds, scooping fish and crustaceans from the water's surface. Flying to stay in one place while supporting the body weight is a difficult feat, and is possible for small birds. Most likely, *Ichthyornis* was a plunge-diver like modern gulls. During foraging, it would hover low over the water to spot prey near the water's surface, plunge-dive into the water to grab the prey, and then rapidly take off again, the prey held tightly in the toothed jaws.

The long and narrow wings of *Ichthyornis* with high aspect ratio are built for gliding and soaring like modern seabirds. *Ichthyornis* was an excellent glider and probably harnessed wind shear—the difference in wind speed at different heights—in a technique called dynamic soaring. The air is quite still near the surface of the sea even when the wind is blowing strongly just a few meters above, so *Ichthyornis* could rise to gain height like a kite in the breeze, then glide down in any direction. By repeating this maneuver it could travel anywhere, regardless of wind direction. *Ichthyornis* probably used dynamic soaring over vast open expanses of the Niobrara Sea while searching for prey and remained airborne indefinitely without flapping its wings. Among Mesozoic birds, *Ichthyornis* shows the most advanced flight structure comparable to that of modern birds and was capable of intricate long-distance maneuvering flight across the continents.

Other than an improved flight apparatus, ornithurine birds developed a specialized nervous system required for active stabilization and control of maneuvering during flight (Maynard-Smith 1952). This is reflected in the evolution of an expanded brain in *Ichthyornis* with architecture close to that seen in modern birds (Jerison 1973). With further enlargement of the brain (EQ ranging from 0.54 to 1.6) and an expanded cerebellum and vestibular system for balance and coordination, the neurosensory control system would be able to constantly and almost instantly correct for minor displacement of the wings (Chatterjee 1997). The vestibular system in ornithurine birds is well developed, with a large flocculus surrounded by three large semicircular canals containing gravity and rotor sensors—like a built-in gyroscope; these are particularly important for maneuvering in flight. The development of maneuvering-flapping flight required integration by the cerebellum of the continuous proprioceptive input from the muscles with input from the motor centers. With the development of skeletal and neurological innovations, ornithurine birds, as exhibited by *Ichthyornis*, were able to make long-distance maneuvering flights.

13 Eggs, Embryos, and Heterochrony

The music of the moon
Sleeps in the plain eggs of the nightingale.

Alfred, Lord Tennyson, *Aylmer's Field*, 1864

Eggs

The avian egg is a marvel of architectural design. Light and strong, it is a self-contained life support system for the developing embryo. Birds inherited amniote eggs from their reptilian ancestors. The watertight amniote eggs evolved in reptiles during the Late Carboniferous time that allowed them to conquer the land. The covering of the earliest amniote shell was most likely a tough, leathery membrane similar to that of a turtle egg. Eventually, hard calcareous shells (like those of chicken eggs) developed in later amniotes when the glands in the uterus began to secrete calcite crystals that would coat the leathery membrane to form a hard and rigid structure. A biomineralized shell prevents fluids from evaporating and protects the growing embryo. Today such eggs are laid by reptiles, birds, and egg-laying mammals such as the platypus; all are grouped in a larger clade, called Amniota. In these animals, fertilization is internal. Amniotes lay their eggs on land, and development is direct from embryo to adult without any intervening tadpole stage. Young amniotes resemble their parents in body form and breathe by means of lungs. The eggshell acts as a protective covering for the embryo as well as an important source of calcium. It is strong enough to hold the embryo securely during development, yet weak enough for the hatchling to break. It is porous enough to permit the respiration of the embryo, yet closed enough to prevent the entry of dirt and microorganisms. The shell provides the mechanical strength of the egg, shielding the embryo from the outside world.

Various components of the amniote egg work together to support the life and growth of the embryo. An amniote egg has a waterproof, calcareous shell that encloses a gas pocket (to allow for expansion or contraction of its contents) and three fluid-filled membranes, the amnion, yolk sac, and allantois, which permit the embryo to survive during development. The outer shell prevents the egg from drying, while an internal membrane, the amnion, encloses the embryo in the watery environment (fig. 13.1). The embryo floats within the amnion, filled with amniotic fluid, which has a composition similar to that of seawater and provides the embryo with a stable fluid environment. The allantois performs two important functions for the embryo: it stores and removes

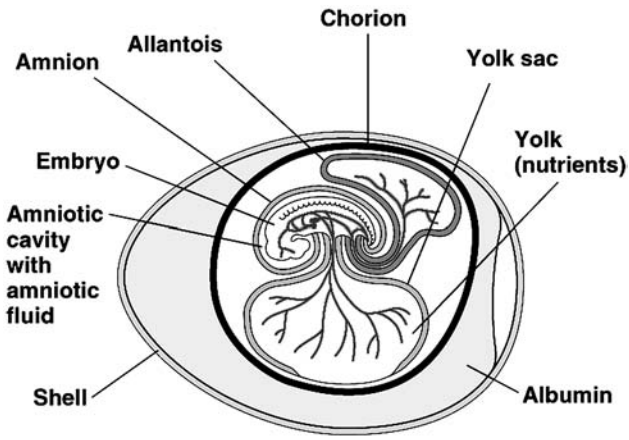


Figure 13.1. The developing embryo inside an egg showing three liquid-filled sacs: amnion, yolk, and allantois. The amnion sac is the characteristic of the amniote egg. The outer shell is semipermeable and is perforated by numerous tiny pores that allow the embryo to breathe.

the nitrogenous waste of the embryo and facilitates respiration. It acts as a lung, taking in oxygen and giving off carbon dioxide. The yolk sac contains a fat and protein-rich yolk that provides food for the embryo. As the embryo matures and feeds on the yolk, the yolk shrinks in size. Surrounding the embryo, amnion, yolk sac, and allantois is the chorion, the inner membrane of the egg that provides an overall enclosure for the embryo. Outside the chorion is the albumin (egg white) of the egg that provides additional nutrients and water and offers a protective buffer from the outside world, which is covered by another membrane. Finally, this outer membrane is encased by an outer calcareous shell that prevents moisture loss and bacterial invasion while permitting gas exchange. The outer shell contains thousands of tiny pores that allow the embryo to breathe—to take up oxygen and discharge carbon dioxide by simple diffusion.

Evolution of Reproductive Behavior

Birds reproduce sexually. All female birds lay eggs. Because eggs are rich in protein and nutrition, a delicacy for many animals including us, birds must find a secure place to lay and hatch their eggs. Birds are unique among living vertebrates in the wide range of developmental strategies and forms of parental care they employ. Birds build their nests to cradle their eggs and young, hiding the helpless offspring from predators.

Because of flight, birds have reduced the reproductive organs in a minimalist way to save weight. Most birds do not have the same reproductive body parts as mammals. Instead, the sex glands, or gonads, of birds consist of paired testes in males and a single ovary in females. Both male and female birds have a cloaca—a posterior opening for the intestinal, urinary, and reproductive tracts. Near the time of mating, the males and females produce sperm and egg cells, respectively. These sexual cells make their way to the cloaca where they reside until mating. Because most birds lack external genitalia, copulation normally involves only brief cloacal contact, a process known as a "cloacal kiss." After sexual stimulation, sperm swim directly to the upper end of the oviduct, where fertilization occurs. In birds, as in all vertebrates, the female reproductive system is generally divided into two separate parts: the ovary (an egg-producing organ) and the oviduct (a tube from the ovary to the outside of the body for passage of the egg). Fertilization converts an ovum into an embryo, which then travels through the oviduct to complete the process of egg formation.

The avian egg is composed of four distinct components: the yolk, the albumen, the shell membranes, and the eggshell. Each component performs specific functions in the development of an embryo. The various components of the egg are formed in the different anatomical regions as the ovum travels through the oviduct. Albumen is the first egg component added to the ovum, followed sequentially by the yolk, the fibrous shell membranes, and the calcareous portion of the shell. Development of a mature ovum includes two processes: the formation and deposition of yolk layer (called vitellogenesis) and the differentiation, growth, and maturation of the ovum. When a full-sized ovum is swollen with yolk, it is ready for the passage down the oviduct. Only a few ova make it to this stage. The final stage of egg production—the addition of a hard calcareous shell—occurs in the region of oviduct called the uterus (fig. 13.2A). Eggshell is largely crystalline calcium carbonate. Calcium is an essential element in the diet of birds, especially for pro-

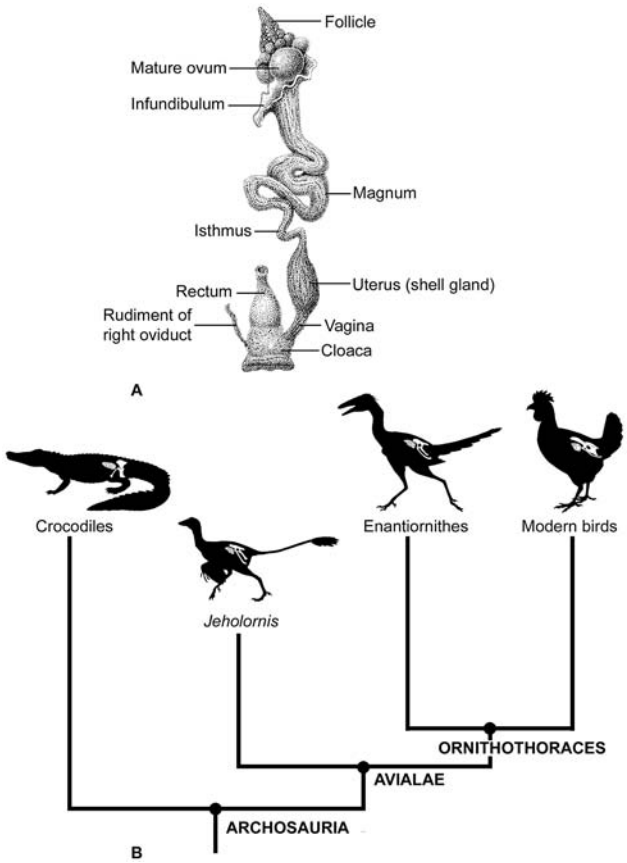


Figure 13.2. Reproductive biology of birds. A, the ovary and oviduct of the chicken are involved in the formation of the egg; the calcareous shell is formed in the uterus of the oviduct during the journey of the fertilized egg; B, phylogeny of the reproductive behavior of archosaurs showing the modification of relative ovary morphology (simplified from Zheng et al. 2013).

ducing eggs; some calcium comes partly from the bird's bones and when necessary from the oviduct during the final stage of egg formation. Without sufficient calcium, eggshells can be defective, causing clutch desertion, as the hatchlings never hatch. The hard shell consists of three layers. The outermost shell is the cuticle or the external zone. Beneath the cuticle is the calcium carbonate layer, the testa or the squamate zone; the innermost layer is the mammillary zone.

There are two living groups of archosaurs, crocodiles and birds, which develop amniote eggs. However, they differ greatly in their reproductive habits in terms of clutch size, nesting behavior, degree of parental care, and developmental strategy of the young. Crocodiles and birds are widely separated phylogenetically. They represent two end members of the reproductive strategies of archosaurs; the gap between them can be filled up by the transitional fossils of theropods and early birds. Crocodilians have two functional oviducts. Female crocodilians are sexually mature when they are ten to twelve years old, and lay about forty to sixty eggs in an hour. Crocodilians reach sexual maturity before the onset of skeletal maturity. In contrast, birds generally possess a single functional oviduct and they reach skeletal maturity before sexual maturity. Modern birds lay one egg every two to six days. They grow rapidly and reach skeletal maturity within one year, but became sexually mature later (two to eight years). The female bird usually carries a single egg in the oviduct, rather than two. There is a great evolutionary advance in reproduction in birds from the crocodilian mode of reproduction, but the details of this transformation remain largely unknown because soft tissues such as reproductive organs are not usually preserved in the fossil record. As a result it is not clear when birds lost their right ovary and oviduct during evolution, but the loss is generally attributed to their overall reduction in body weight in response to flight, especially during reproductive season for the females. Recent spectacular discovery of soft tissues such as ovarian follicles in feathered theropods and early avialans from the Early Cretaceous Jehol Group of China sheds critical light on the evolution of egg production in early birds (Zheng et al. 2013).

From the Chinese fossilized ovarian follicles it becomes clear that both crocodilians and advanced maniraptoran theropods retain paired ovaries, but modern birds have a single ovary, the left one. Zheng et al. (2013) provided the critical evidence to pin point when the right ovary was lost in early birds in a phylogenetic context (fig. 13.2B). The ovary of these early avialans resembles a small cluster of grapes, called follicles, which are preserved in rows at the posterior end of the sternum and pelvis. Unfortunately, the oviduct is not preserved in these specimens of avialans. Previous discovery of the paired association of eggs in the body cavity of one ovi-

raptoran specimen from China suggests that nonavian maniraptorans had two active oviducts. Most likely during the transition from theropods to early birds, the right ovary was lost to reduce body weight for active flight.

The follicle patterns of two important clades of ancient birds—primitive long-tailed, gliding avialans (such as *Jeholornis*) and small, tailless, and highly acrobatic enantiornithines—fill critical gaps in reproductive behavior between crocodiles and modern birds (fig. 13.2B). In *Jeholornis*, the size and distribution of follicles show a mosaic of primitive and advanced reproductive strategies. The follicles exhibit early stages of vitellogenesis in preparation for ovulation; they matured simultaneously as in crocodilians. Also, *Jeholornis* reached sexual maturity before skeletal maturity as do crocodiles and dinosaurs. The large clutch size indicates a precocial reproductive strategy and that young needed little parental care. However, *Jeholornis* hints at the presence of a single functional left ovary as in modern birds, which is consistent with its flight adaptation.

In the more derived enatiornithine clade, as the animals became small and sparrow-sized, efficient at perching and acrobatic flying, reproductive behavior retained primitive traits as in avialans. For example, in this lineage, sexual maturity was achieved before skeletal maturity as in crocodilians and avialans, probably linked with lower metabolic rate and slow growth. These birds retained a precocial mode of development. In modern birds, with fast growth and small clutch size, we see the acme of reproductive behavior. Modern birds reach sexual maturity within one year, but become sexually mature later, between two and eight years of age. The number of ovarian follicles is relatively small in modern birds compared to that in fossil forms, but each follicle is relatively large, indicating small clutch size with relatively large eggs. Most likely, the future discovery of ornithurine fossil follicles from China will fill this important gap in reproductive strategy.

Size and Shape of Avian Eggs

The kind of egg that a bird lays depends on how it lives. Birds lay one egg at a time. The shape, color, and number of eggs vary greatly among birds. Although bird eggs appear to be fragile, they are in fact extremely robust. Most bird eggs are ovoid like those of the chicken, with one end rounded and the other pointed to facilitate its movement through the oviduct. Moreover, the convex exterior can withstand more pressure, especially during hatching. Long and pointed eggs are found in woodpeckers and swifts, while spherical eggs occur in birds such as kingfishers and owls. There are several transitional forms between these two extremes. Wading birds lay more eggs, which are camouflaged to match the surrounding coasts and inlets to avoid detection. Small landbirds lay diminutive eggs in large clutches. Large birds, on the other hand, lay far fewer eggs. True seabirds usually lay a single egg on precarious rocky ledges to deter enemies.

The default color of an avian egg is white because calcium carbonate, the mineral that constitutes the outer shell, is white. Two common pigments in avian eggs are bilverdin and protoporphyrin; the former gives a green or blue ground color, the latter hues of red and brown for ground color or for spots and speckles. Coloration is an integral part of the development of an egg, mediated by a gene. The pigment is deposited on the shell during its passage to the oviduct. White eggs often belong to birds such as owls and kingfishers that nest in dark and enclosed spaces such as holes or burrows. All parrot species have white eggs. Birds that build nests in trees have blue or greenish eggs. Most eggs laid in open nests are speckled, spotted, blotched, or lined. The color varies considerably to camouflage eggs that lay on the ground. Some of the large flightless birds lay colorful eggs that blend in with the ground: ostriches lay white eggs, rheas have creamy, beige eggs, and emus have greenish-black eggs, while tinamous lay shiny, emerald green eggs.

Avian eggs vary greatly in size, which is influenced by the amount of yolk. The bigger the yolk, the bigger is the size. Egg size is also related to bird size, but the relationship is much more complex. Hummingbirds (3 grams) lay the smallest eggs (0.3 gram, about 10% of body mass), and ostriches (100 kilograms) lay the largest (1 kilogram, about 1% of body mass). If we compare these two extreme birds, there is a 3,000-fold range of increment

in egg mass, but the body mass increases 30,000-fold. Thus, larger birds lay proportionately smaller eggs relative to their body size. The largest known egg is that of the extinct flightless elephant bird, *Aepyornis* of Madagascar (500 kilograms). Its egg measured 34 by 24 centimeters and weighed about 10 kilograms. It could hold the contents of 7 ostrich eggs, 180 hen eggs, or 50,000 hummingbird eggs. It becomes apparent that the relationship between body weight and egg weight is exponential in a fashion similar to that between body weight and brain weight; body mass increases more rapidly than egg mass. H. Rahn and his colleagues plotted bird egg mass against body mass on logarithmic coordinates and deduced the following allometric equation (Rahn et al. 1975):

$$\text{egg mass} = 0.277\ (\text{body mass})^{0.77}$$

As a rule, large eggs have thick shells and small eggs have thin shells. The eggshell is largely made of polycrystalline calcite minerals held in a matrix of collagen fibers. The microscopic structure of the shell in radial section reveals two main layers—an inner mammillary layer and an outer spongy, or palisade, layer. The mammillary layer is composed of numerous roughly conical knobs, or mammillae, which are oval to circular in cross section with an organic core. They are tightly compressed side by side in a single stratum. The spongy layer is thicker, with calcite crystals arranged in the protein matrix as vertical palisades separated by minute pore canals. The chicken egg contains about 10,000 pores, which permit gas exchange (Rahn et al. 1979). The outer surface of this calcite layer is overlain with a protein cuticle that gives it a smooth, shiny appearance.

Eggshell Structure

Baby dinosaurs and dinosaur eggs have long been a source of fascination to both paleontologists and the public. A wide array of dinosaur eggs of different sizes and shapes, some in nests and some isolated, are known from various parts of the world. In the past few decades, a series of spectacular discoveries of eggs, nests, embryos, and nestlings have provided valuable insights about the reproduction and parenting behavior of dinosaurs. The new evidence suggests that some dinosaurs not only tended their eggs but cared for their young as well. This is not surprising because parental care of eggs and young occurs universally between two extant archosaurs, crocodilians and birds. The modern analogues for comparing dinosaur-nesting behavior are living archosaurs such as crocodilians and flightless birds that lay eggs on the ground, guard their nests, and exhibit fairly extensive parental care. These eggs have hard, somewhat brittle, and largely calcitic eggshells, and need to be incubated at a correct temperature for embryonic growth. The incubating temperature is generated either by the environment (microbial decomposition of vegetation, solar radiation, geothermal heat) or by the body heat of the parent. Dinosaurs might have used both incubation strategies (fig. 13.3).

The wide variety of nest construction suggests that female dinosaurs laid hard-shelled eggs, which were arranged either in circular clutches or in linear rows that were dug in the soil, and then covered with a thin layer of vegetation or sediment for incubation. To arrange eggs in a specific pattern requires a great deal of precision, planning, and care by the parent. Dinosaurs deposited a variable number of eggs, ranging from ten to thirty eggs per nest. Some dinosaurs grouped their nests in breeding colonies, and certain species returned to the same nesting site year after year. Dinosaurs constructed a wide variety of nests, ranging from simple holes in the ground to more complicated mounds. About two hundred nest sites have been found around the world. Most date from the Cretaceous period, but few of them contain developing embryos and hatchlings that provide the identity of the egg-layers.

The hard eggshell is largely composed of an inner, organic shell membrane and an outer calcareous layer of polycrystalline calcite minerals held in a matrix of collagen fibers. The microscopic structure of the shell in radial section reveals a variation in the number of layers among dinosaurs: a single layer is found in sauropods and ornithischians, two distinct layers in theropods, and three layers in birds. Pore canals pass through the shell to permit embryonic gas exchange. The size and shape

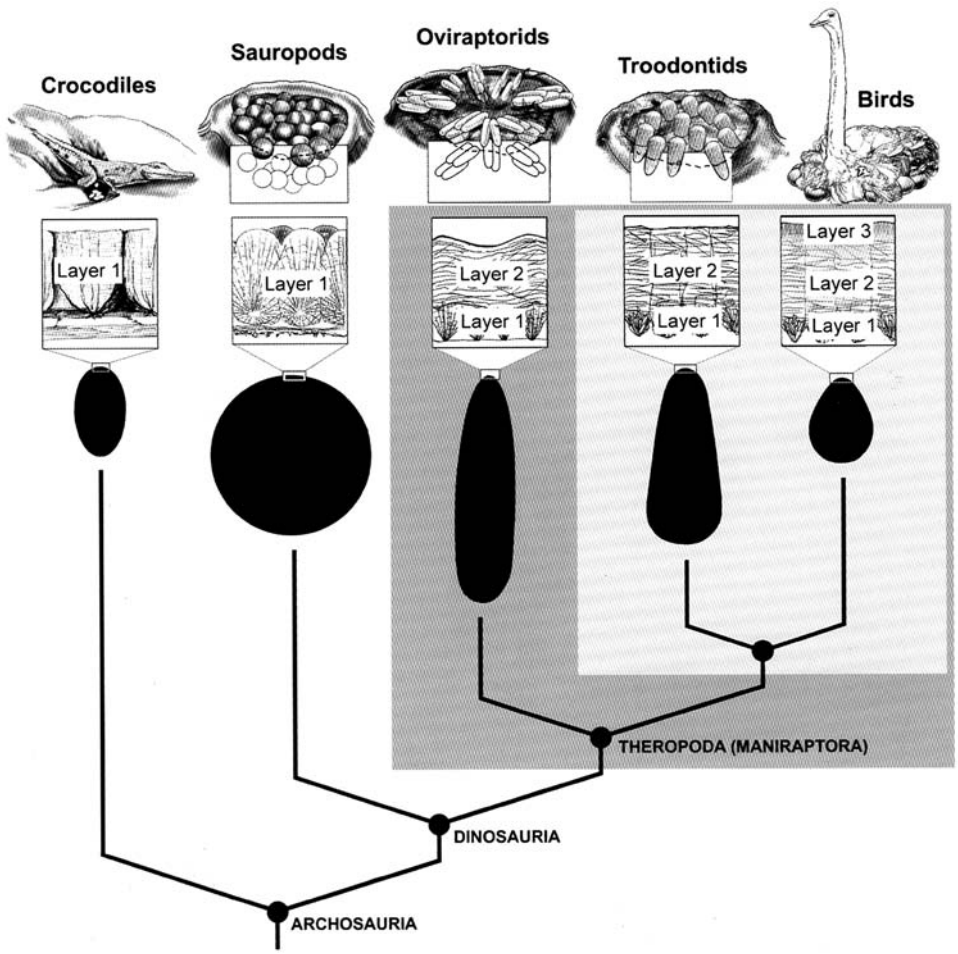


Figure 13.3. Variations of size, shape, clutch, and microstructures of eggshells among several lineages of archosaurs and modern birds. The microstructure of eggshell in radial section in both crocodilians and sauropods shows a single layer (basal mammillary layer); the addition of layer 2 (squamate zone) occurs in maniraptoran theropods; and layer 3 (external zone) is added in bird eggshells (after Chiappe 2007, with permission from the author).

of eggs vary among different groups of dinosaurs. Sauropod eggs are large and spherical, but theropod and ornithischian eggs are variable, ranging from elongated ellipsoid to oval to spherical. The fossil egg is often difficult to link to a specific dinosaur, but the size and shape of the eggs, the shell thickness, the pore pattern, and the microstructures of eggshells provide tantalizing clues to which kind of dinosaurs might have laid the eggs. In rare cases, the embryos or hatchlings might be present in a nest and provide positive identification of the producer of the eggs.

Despite the dramatic discovery of feathered dinosaurs and early birds from the Early Cretaceous deposits in China over the past decade, our knowledge of egg morphology and nesting behavior in Mesozoic birds remains sparse. Avian fossil eggs from the Mesozoic sediments are extremely rare, known thus far only from the Late Cretaceous Barun Goyot Formation of the Gobi Desert of Mongolia. The Russian paleontologist Konstantine Mikhailov (1992) has worked on this Gobi eggshell material. He recognized two kinds of avian eggs associated with embryos. The first type of egg is about 40 millimeters long and 20 millimeters wide. It is a small, ovoid egg belonging to a neornithine bird, *Gobipipus*. The eggs are found with their narrower end down, either vertically or obliquely in the sediment (fig. 13.4A–B). The second type of egg is rela-

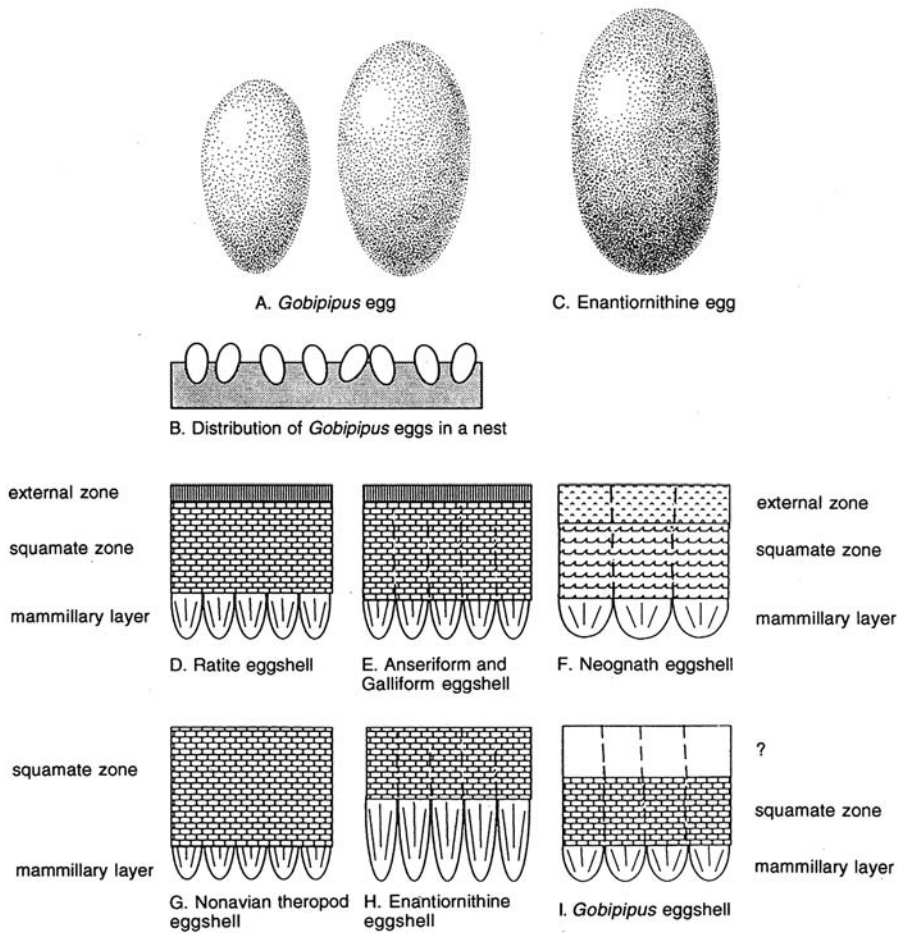


Figure 13.4. Eggshell and microstructure. A, two varieties of asymmetrical (ovoid) eggs are attributed to *Gobipipus*; the smaller variety is about 30–46 millimeters long, whereas the larger one is about 53–70 millimeters long. B, distribution of *Gobipipus* eggs in a single stratigraphic layer and their subvertical position in the substrate. C, the symmetrical (ellipsoidal) egg of *Laevisoolithus* probably belonged to an enantiornithine bird. D–I, general variants of ornithoid eggshell structure in radial section, based on data from scanning electron microscopy (SEM). Three structural strata of eggshell are shown diagrammatically: a basal mammillary layer, a middle squamate zone, and an outer external layer; vertical dashed lines indicate the expressiveness of columns in the continuous or spongy layer (simplified from Mikhailov 1992). D–F, modern bird eggshells: D, ratite eggshell; E, anseriform and galliform eggshell; F, typical neognath eggshell. G–I: fossil theropod eggshells: G, nonavian theropod eggshell (Oofamily Elongatoolithidae); H, enantiornithine eggshell (Oofamily Laevisoolithidae); I, *Gobipipus* eggshell (diagenetically altered zone) (simplified from Kurochkin et al. 2013).

tively large, about 70 millimeters long and 40 millimeters wide. It has a symmetrical ellipsoidal shape and is attributed to an enantiornithine bird (fig. 13.4C).

Mikhailov studied the microstructure of dinosaur and avian eggshells under a scanning electron microscope. He recognized three horizontal strata, or zones, of microstructure in avian eggs from the inner to the outer surface: (1) a basal mammillary layer with radial organization of biocrystalline material, (2) a middle continuous or spongy layer with polycrystalline squamatic ultrastructure, and (3) an outer external zone (fig. 13.4D–I). Mikhailov proposed two morphotypes for the avian eggshells, Ratitae and Neognathae, emphasizing the microstructure of the spongy layer. In the ratite morphotype (as seen in ratites, galliforms, and anseriforms), the squamate layer does not exhibit distinct columns and the external zone is a dense crystalline layer (fig. 13.4D–E). In the neognathous morphotype, which is the most preva-

lent among living birds, the squamate layer exhibits distinct columns and prisms (fig. 13.4F). Interestingly, both types of Cretaceous eggshells from the Gobi Desert show a microstructure of the ratite morphotype (fig. 13.4H–I).

Embryos

Ontogeny, the development of the individual from egg to adult, is an important component of evolutionary study. Birds employ a wide range of developmental strategies and forms of parental care. Avian hatchlings display remarkable differences in their skeletal morphology, external appearance, activity, and behavior. Some birds can fly shortly after hatching and are independent of parents. Others are born prematurely and need constant parental care and feeding until they become self-sufficient. The study of fossil eggs, nests, and embryos provides insights into the early developmental history of birds from growth to family life.

Embryonic skeletons of birds are certainly among the rarest of fossils. In 1971, a joint Polish-Mongolian team discovered several avian nesting sites in the Upper Cretaceous Barun Goyot Formation of Khermeen Tsav in the southern Gobi Desert in Mongolia, along with a rich trove of nonavian dinosaurs and mammals. Many of these avian eggs contain precocial embryonic skeletons, which were described by Anjay Elzanowski (1981). Precocial birds are capable of a high degree of independent activity from birth. Various specimens show partial skulls, wings, shoulder girdles, vertebrae, and parts of the hindlimbs. Elzanowski concluded that these embryonic specimens belonged to an enantiornithine bird, *Gobipteryx minuta*, which he described earlier from an adjacent area (fig. 13.5A–B).

Another new embryonic bird has been described recently from the Gobi Desert on the basis of two specimens (Kurochkin et al. 2013). Valeri Reshetov found the specimens on the eastern side of Khermeen Tsav in 1977. In the first specimen the skeleton, preserved in exquisite detail, is in a fetal position revealing the skull, the shoulder girdle, the wings, and a series of neck vertebrae (fig. 13.5C–D). The second specimen shows a partial hip girdle and hindlimb (fig. 13.5E). Surprisingly, most of the bones are well ossified, indicating that the embryos were close to hatching (fig. 13.5F). I have named this bird *Gobipipus reshetovi* as another member of the enantiornithine birds. *Gobipipus* is a basal member of enantiornithine birds and shares more features with ornithuromorph birds than previously recognized. Although both *Gobipipus* and *Gobipteryx* are toothless enantiornithine birds and both are known from the same Late Cretaceous horizons of Gobi Desert, these taxa are quite distinctive in morphology.

Early evolutionary biologists have recognized the importance of understanding how animals grow and develop and the functions of parental care in the survival of birds for more than a century. In regard to their maturity at hatching, there are two broadly different types of birds: altricial and precocial. Altricial chicks are born helpless, blind, naked, and feeble, and they are completely dependent on parental care (fig. 13.6A). At the other extreme are precocial chicks, born fully feathered, alert, bright-eyed, and able to run after their parents and feed themselves independently (fig. 13.6B). The fundamental functions of parental care are, of course, protection and provision of nourishment. By staining bone and cartilage, J. Mathias Starck (1993) has studied in detail the patterns and sequence of ossification of a wide range of embryonic birds and has found two different styles. The skeletons of precocial birds, which move actively but grow slowly, show a high proportion of bone and a low percentage of cartilage. Conversely, the skeletons of altricial birds, which grow quickly, show a high proportion of cartilage and a low percentage of bone. Interestingly, both *Gobipteryx* and *Gobipipus* show a high degree of ossification in the embryonic stage, suggesting a precocial mode of development (fig. 13.6B). It is likely that the hatchlings of both genera were able to fly as soon as they emerged from their eggs, as is evident from their ossified wing skeletons. Starck concluded from his ontogenetic analysis that the precocial mode of development is primitive for birds, whereas the altricial mode is more advanced. Cretaceous embryos from the Gobi Desert support this contention. In these birds, the bones are so well ossified that the hatchlings probably were self-sufficient and steady on their feet from the beginning and fed themselves.

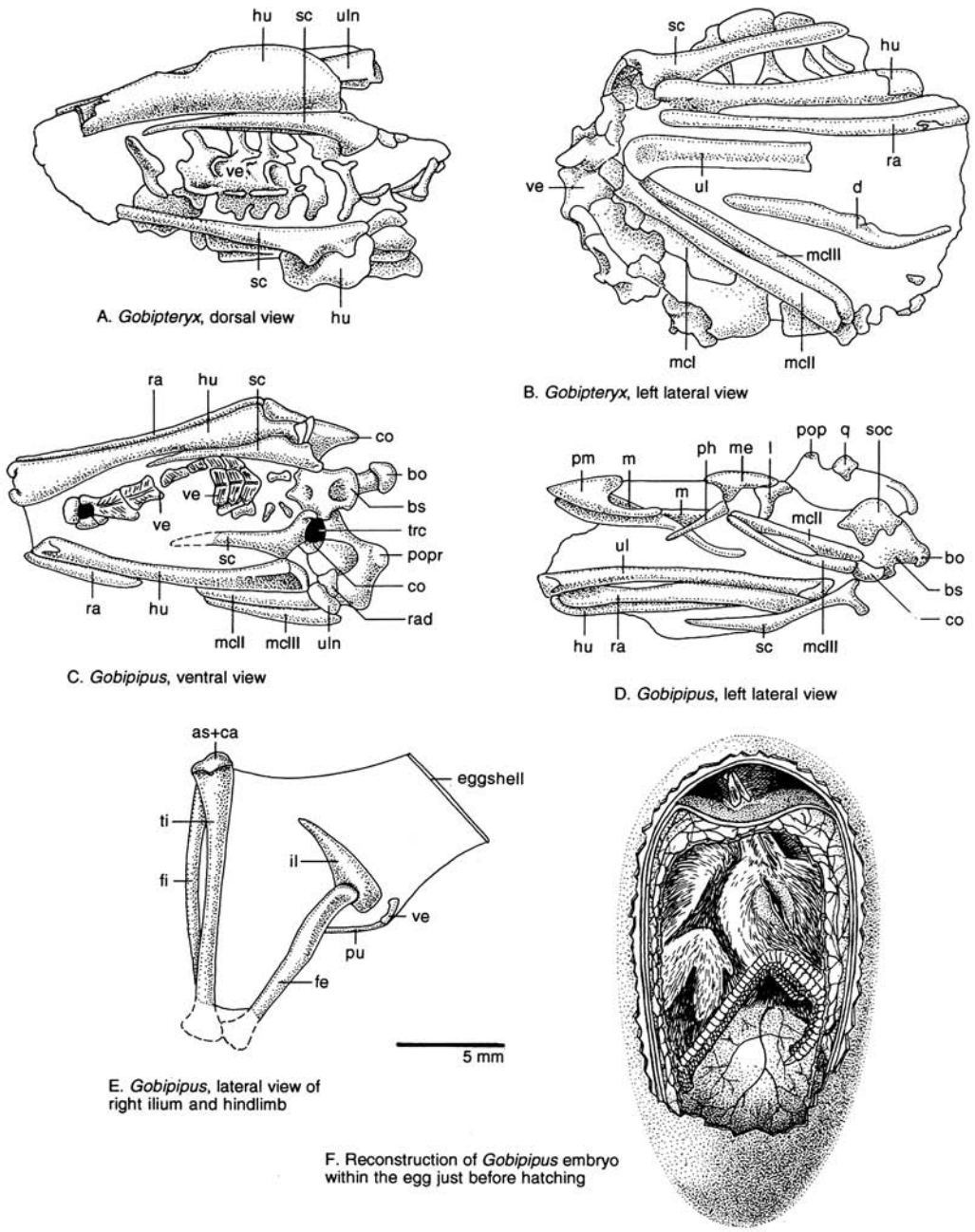


Figure 13.5. Embryos of Late Cretaceous birds from the Gobi Desert, Mongolia. A-B, *Gobipteryx minuta*, dorsal and left lateral views (simplified from Elzanowski 1981). C-D, ventral and left lateral views of *Gobipipus reshetovi*; the delicate skeleton in a fetal position is about 18 millimeters long, showing a partial skull, vertebrae, the shoulder girdle, and wing elements. E, *Gobipipus reshetovi*, lateral view of the right ilium, femur, tibiotarsus, and fibula. F, this reconstruction shows a 35-millimeter-long *Gobipipus* embryo just before hatching (C-F, after Kurochkin et al. 2013). For abbreviations, see figures 5.4-5.9.

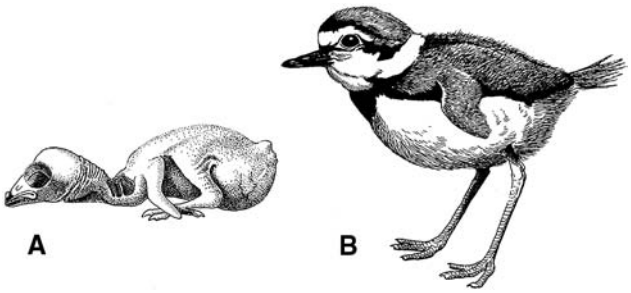


Figure 13.6. Altricial versus precocial mode of development among recent birds. A, the one-hour-old chick of an altricial bird, the Java sparrow (*Lonchura oryzivora*), is blind, naked, and utterly helpless. Most tree-nesting and cavity-nesting birds have altricial chicks, which require long periods of feeding before they are strong enough to leave the nest on their own. B, the one-hour-old chick of a precocial bird, the killdeer (*Charadrius vociferus*), by contrast, has open eyes and a thick coat of natal down and is able to fend for itself. Most shorebirds, gamebirds, and ducks have precocial chicks, which can walk away from the ground nest within hours of hatching.

They could even fly when they were quite small, similar to modern gallinacious birds. This is no doubt a useful safety device for terrestrial birds. These birds probably buried their eggs in the ground and gave little parental care to the chicks. Altriciality is a more sophisticated mode of development, which might have evolved later in the evolution of birds, when eggs were placed in an arboreal nest with associated parental care. Altricial birds lay relatively larger eggs than their precocial counterparts.

The Role of Heterochrony in Avian Evolution

Heterochrony—change in the timing or rate of developmental events—has been linked to the evolution of major vertebrate lineages. It is the missing link between genetics and natural selection, providing the raw material on which natural selection works (McNamara 1977). Development reflects the storage of historically acquired characters, mediated by genetic tool kits. The interplay of development and evolution has been a central theme in evolutionary theory for more than a century. It has long been known that there is a close correspondence between the development of the individual from egg to adult (ontogeny) and the ancestry of species (phylogeny), but the nature of this relationship is far more complex than is usually believed. Soon after the publication of *On the Origin of Species,* the German biologist Ernst Heinrich Haeckel (1866), an ardent supporter of Darwinism, proposed his famous biogenetic law, which states that "ontogeny recapitulates phylogeny." Haeckel believed that, in the course of development, each kind of animal repeats all of the stages of its evolutionary history. Thus, adult characters of ancestors become the juvenile characters of descendants, but they are crowded back into earlier stages of ontogeny. Haeckel proposed that phylogeny literally causes ontogeny through two processes: terminal addition, which adds new features to the end of ontogeny, and condensation, which deletes earlier ontogenetic stages to make room for new features (Gould 1977). Haeckel was aware of exceptions to his biogenetic law, and coined the term "heterochrony" to explain evolutionary change in the timing or rate of developmental events. Later, Gavin de Beer (1958) clarified some of the misconceptions of recapitulation and showed other relations between embryonic development and evolutionary descent. For example, in many evolutionary lineages, adult descendants retain ancestral juvenile characters. If sexual maturity occurs earlier in the descendant than in the ancestor, a juvenile morphology occurs in the descendant adult. These descendants superficially look like "degenerate" forms that passed through fewer morphological stages during their development than did their ancestors. De Beer termed this evolutionary pattern "paedomorphosis," meaning "child formation."

There has been a great deal of interest in synthesizing the relationship between ontogeny and phylogeny, with better definitions and formalisms (Gould 1977; Alberch et al. 1979; McKinney and McNamara 1991; Livezey 1995). These studies have revealed how ontogeny, the internal influence, can play a major role in the evolutionary process along with external influences, such as natural selection. Evolution can thus be thought of as a triangle, with genetics and heterochrony forming the basal corners and natural selection the vertex (McNamara 2001). The pervasive force behind the evolution of morphological innovations lies in developmental plasticity. Variation in developmental constraints may filter novel adaptive

character states on which selection may act. By altering the ontogenetic sequence through which ancestors had developed, heterochrony can create morphological novelties in descendant adults. During ontogeny, structures can be added or subtracted from those of ancestors, or changes can be accelerated or retarded.

In summary, heterochrony implies differences in the developmental timing of features relative to the same events of the ancestor. It may affect a wide range of developmental phenomena. Heterochrony produces two forms of morphological expression: (1) peramorphosis (more overdevelopment), where ancestral adult characters appear in the descendant juvenile (recapitulation); and (2) paedomorphosis (less development), where the descendant adults retain ancestral juvenile characters (fig. 13.7). Gould and his colleagues (Alberch et al. 1979) recognized six heterochronic processes that involve changes in shape and size: three within peramorphism and three within paedomorphism. Peramorphism is produced by three ontogenetic mechanisms: acceleration (faster growth rate), hypermorphosis (late finishing), and predisplacement (earlier starting); the corresponding paedomorphic processes are neoteny (slower growth rate), progenesis (early finishing), and postdisplacement (delayed starting). Many authors have speculated that both progenesis and neoteny have been important in the origin of higher taxa (Garstang 1922; de Beer 1958; Gould 1977). During ontogeny, structures can be added or subtracted from those of ancestors, or changes can be accelerated or retarded to produce new anatomical features and species.

Heterochrony has played a significant role in the evolution of birds on three-tier hierarchical levels, which has never been explored before. The first tier of heterochrony is documented in the early evolution of avialans such as *Archaeopteryx* and *Jeholornis* from theropod ancestors. Since *Archaeopteryx* and *Jeholornis* have similar body plans and proportions, but the former is better known anatomically, I will use *Archaeopteryx* as a basal member of avialans to explore the first tier of heterochrony, supplemented by *Jeholornis* when possible. Heterochrony at this level is a mosaic of peramorphic and predominant paedomorphic trends. The driving force behind this heterocline was the progressive evolution of flapping flight by small, arboreal feathered coelurosaurs with the acquisition of miniaturization of size. The paedomorphic features include the small body size, large orbits, an inflated braincase, a short snout, reduction of tooth count, subconical and unserrated teeth, an unossified uncinate process, and loss of the metatarsal wing. Small size was advantageous for a novice flier by decreasing wing leading and improving the power-to-mass ratio. The peramor-

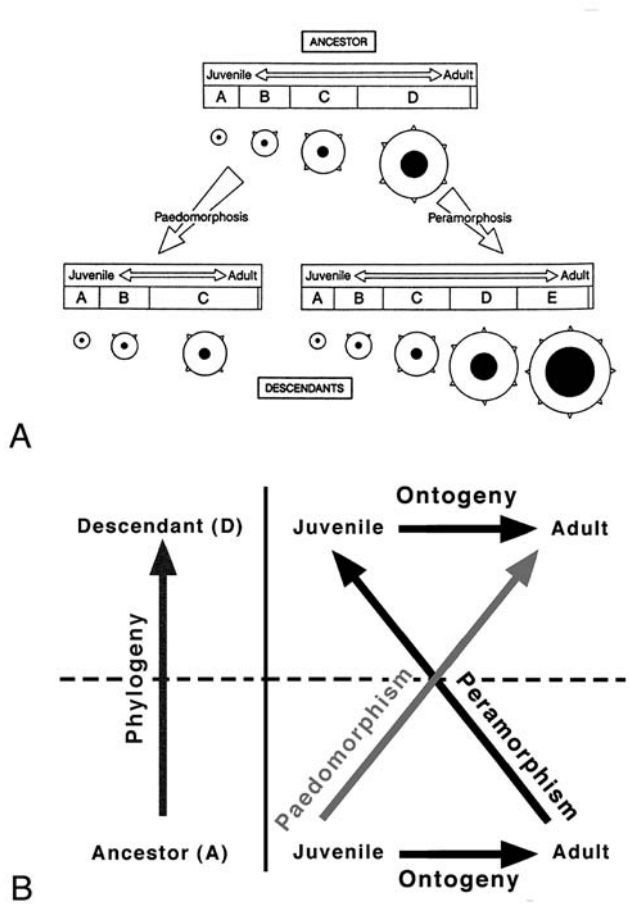


Figure 13.7. Heterochrony. A, shape changes are created by two basic processes: paedomorphosis and peramorphosis. In paedomorphosis, the descendant adults retain ancestral juvenile characters. In peramorphism, ancestral adult characters appear in the descendant juvenile. Here, the descendant adult passes morphologically beyond that of the ancestor, so that in effect, an extra developmental stage is added to the life history (simplified from McKinney and McNamara 1991). B, diagrammatic representation of heterochrony showing the relationships between ontogeny and phylogeny.

phic features comprise elongation of forelimbs relative to hindlimbs, a dorsolaterally faced glenoid, an opisthopubic pelvis, rostral elongation of the preacetabular process, and six sacrals in the synsacrum.

The second tier of heterochrony can be observed from the evolution of neognaths from early avialans such as *Archaeopteryx* and *Jeholornis*, bridging the gap between Avialae and Aves, which is dominated by peramorphism, possibly by acceleration. The peramorphic features include the confluence of the orbit with both upper and lower temporal openings leading to preorbital kinesis; closure of the cranial sutures; heterocoelous centra; an ossified uncinate process; fusion of pelvic girdle elements; elongation of the coracoid; enlargement of the sternum with a deep ventral keel; fusion of the carpometacarpus, tibiotarsus, and tarsometatarsus; reduction of the fibula; loss of ungual claws; reduction of manual digits; and truncation of the tail. The selection pressure for the second level of heterochrony was the fusion of bones for strength and rigidity in response to maneuvering flight with endurance and safe landing. On the other hand, the enlargement of the brain and altricial development may represent paedomorphic traits.

The third tier of heterochrony is encountered in the evolution of modern flightless birds from their flying ancestors by paedomorphism. Flightlessness is a recurrent theme throughout the evolution of birds (see chapter 12), but my discussion will be centered on modern birds. Here the heterochrony is disassociated, showing a combined effect of increased body size and pelvic peramorphism, and more significant pectoral paedomorphism. The selection pressure for this heterochrony is the refinement of cursorial adaptation in flightless birds in the absence of predators.

Level 1. Heterochrony from Ceolophysids to Avialans

Although the phylogeny of theropods leading to early birds is becoming more robust with the continued discovery of feathered coelurosaurs from China, ontogenetic and allometric data for nonavian theropods are still sparse. Recent work on bone histology indicates that basal theropods such as *Syntarsus* reached maturity after seven years (Chinsamy 1992), whereas *Troodon*, a closer relative of *Archaeopteryx*, matured more quickly (after three to five years) (Varricchio 1993). Apparently, all nonavian theropods grew at accelerated rates relative to the primitive condition seen in extant reptiles. Adult *Archaeopteryx* (Solnhofen specimen) reached a body length of approximately 0.6 meter and a mass of about 0.6 kilogram (Chatterjee and Templin 2003), smaller than its closest relative, the 1-meter-long *Microraptor* with a mass of about 0.95 kilogram (Xu et al. 2003; Chatterjee and Templin 2004b). The early birds apparently attained small body size by shortening the phase of rapid growth common to their larger dromaeosaurian relatives (Padian et al. 2001). There is a trend of acceleration of development, a paedomorphic feature in the evolution of early birds from their theropod ancestors. This trend continues in modern altricial birds, which attain maturity very rapidly, in less than a year, as soon as the wings become functional (Starck 1989; Ericson et al. 2001).

Data on ontogenetic development in nonavian theropods are limited. Colbert (1990, 1995) focused on the allometric growth of *Coelophysis*, Madsen (1976) on *Allosaurus*, Russell (1970) on tyrannosaurs, Norell et al. (1994) on embryonic skeletons of *Oviraptor* and *Velociraptor*, Varricchio et al. (1999) on embryos of *Troodon*, Chiappe et al. (2002b) on juvenile alvarezsaurids such as *Shuvuuia*, and Geist and Jones (1996) on the reproductive habits of nonavian theropods. Anatomical changes of juvenile (Eichstätt) and adult (Berlin) specimens of *Archaeopteryx* are also useful in assessing the developmental growth pattern.

Some of the ontogenetic changes observed in nonavian theropods are as follows:

1. increase in size
2. increase in snout length relative to skull length
3. decrease in orbital diameter relative to skull length
4. increase in tooth row length relative to skull length
5. increase in tooth count
6. change of tooth morphology from an unserrated, conical type to a laterally compressed, serrated form

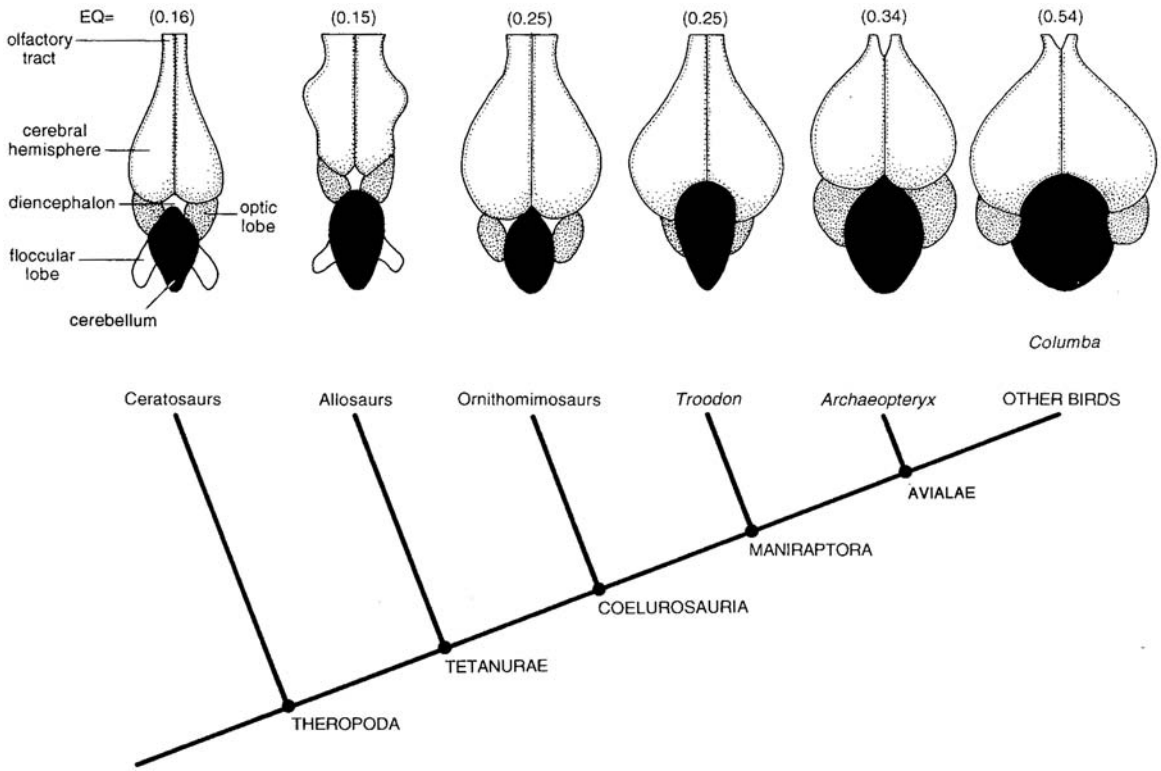


Figure 13.8. Paedomorphic trend in the evolution of brain size in *Archaeopteryx*. A phylogenetic sequence of dorsal view of the brains of major groups of theropods from the primitive stem-group theropod ceratosaur to the modern pigeon showing the progressive increase of the relative brain size and encephalization quotient (EQ). The size of the forebrain, which controls most sensorial perceptions, doubled from *Allosaurus* to *Troodon*. In basal avialans such as *Archaeopteryx* the cerebellum, which controls coordination and balance, increased substantially and makes contact with the cerebral hemispheres. The architecture of the brain of *Archaeopteryx* closely resembled that of modern birds in dominance of vision and hearing, but the larger relative brain size may be a paedomorphic feature. In extant archosaurs, there is a trend toward decreasing relative brain size with age.

7. reduction of the ascending process of the jugal and failure to contact the postorbital in the juvenile form, but an intact diapsid arch in the adult
8. elongation of the forelimb relative to the hindlimb

It is expected that the relative brain size and the orbit in young individuals would be proportionately larger than in older individuals. The encephalization quotient (EQ) data of theropod ontogeny are not known, but using the *extant phylogenetic bracket* (EPB) approach (Witmer 1995), we can infer the allometry of brain size from two most proximal living outgroups of the fossil taxon concerned. For example, if we want to know the EQs of *Archaeopteryx* during growth, we can bracket *Archaeopteryx* between two living archosaur taxa, crocodilians and living birds. Ontogenetic data on *Alligator* and birds are available containing brain mass versus body mass (Crile and Quiring 1940). Using these data, Chatterjee (1991) estimated the encephalization quotients (EQs) of various archosaurs. There is a trend of decreasing relative brain mass with age; the smaller the animal, the larger the relative brain size. In *Alligator*, the EQ changes from 0.28 (mass = 0.35 kilogram) to 0.033 (mass = 205 kilograms) as the animal grows. In *Gallus*, the EQ reduces from 0.71 to 0.2 as the animal grows from 0.046 to 2.2 kilograms. The body mass of archosaurs is inversely correlated with the EQs during ontogeny (fig. 13.8).

The ontogenetic data for *Coelophysis* show a relative reduction in orbit size in the sequence from smaller to larger specimens (fig. 13.9). Side by side, there is a pro-

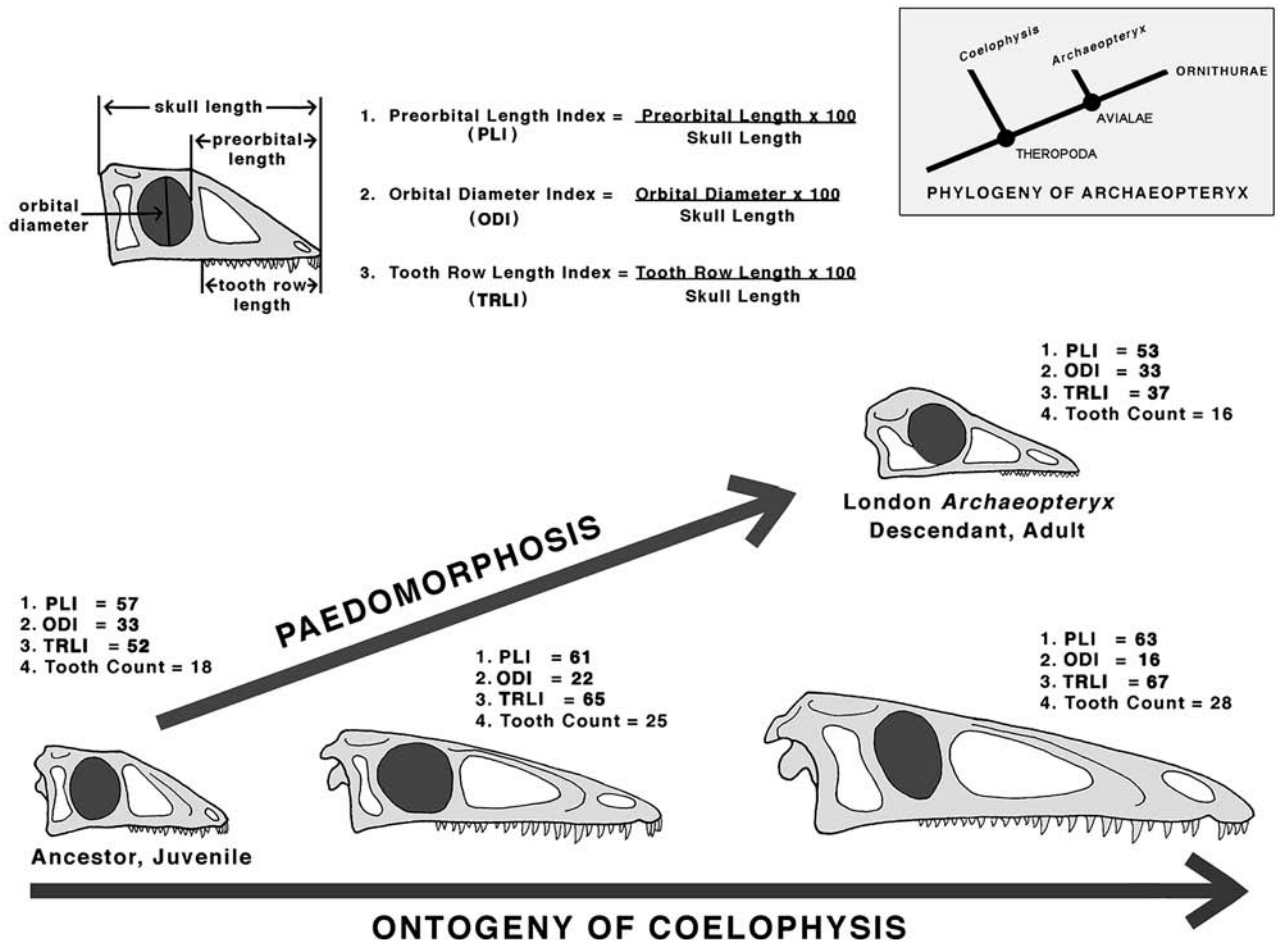

skull length
preorbital length
orbital diameter
tooth row length
1. Preorbital Length Index = Preorbital Length x 100 / Skull Length (PLI)
2. Orbital Diameter Index = Orbital Diameter x 100 / Skull Length (ODI)
3. Tooth Row Length Index = Tooth Row Length x 100 / Skull Length (TRLI)
Coelophysis
Archaeopteryx
ORNITHURAE
AVIALAE
THEROPODA
PHYLOGENY OF ARCHAEOPTERYX
1. PLI = 53
2. ODI = 33
3. TRLI = 37
4. Tooth Count = 16
London Archaeopteryx
Descendant, Adult
PAEDOMORPHOSIS
1. PLI = 57
2. ODI = 33
3. TRLI = 52
4. Tooth Count = 18
1. PLI = 61
2. ODI = 22
3. TRLI = 65
4. Tooth Count = 25
1. PLI = 63
2. ODI = 16
3. TRLI = 67
4. Tooth Count = 28
Ancestor, Juvenile
ONTOGENY OF COELOPHYSIS

Figure 13.9. Paedomorphic trend in the evolution of the skull of *Archaeopteryx* from nonavian theropods such as *Coelophysis*. Characters such as large orbits, a short snout, reduction of tooth count, and the short tooth row length in *Archaeopteryx* are also present in the juvenile *Coelophysis*.

gressive increase of the relative tooth row length as well as the total tooth count as the animal grows in size.

Compared with nonavian theropods, the skeleton of *Archaeopteryx* is somewhat smaller and more streamlined, a paedomorphic trait that was presumably a flight adaptation against gravity. Miniaturization of size is considered a paedomorphic trait. The small body size, arising from progenesis, might be linked with r-selected strategies. The paedomorphic trends in the evolution of *Archaeopteryx* (and *Jeholornis*) from theropod ancestors appear to have operated in the opposite way of ontogeny. The paedomorphic features are as follows:

1. small body size
2. enlargement of the brain (fig. 13.8)
3. a large orbit (fig. 13.9)
4. a short snout (fig. 13.9)
5. reduction of the tooth count (fig. 13.9). In *Jeholornis*, only three small teeth are present in the dentary, but none are present in the premaxilla and maxilla (Zhou and Zhang 2003).
6. subconical, unserrated teeth (fig. 13.10)
7. reduction of the ascending process of the jugal and failure to contact the postorbital as seen in the juvenile specimen of *Shuvuuia* (Chiappe et al. 2002b). As a result, the orbit becomes confluent with the lower temporal opening (fig. 13.11). This is the initial stage of developing cranial kinesis (Chatterjee 1991).
8. loss of the ventral (metatarsal) wing from the biplane wing planform of *Microraptor* (Chatterjee

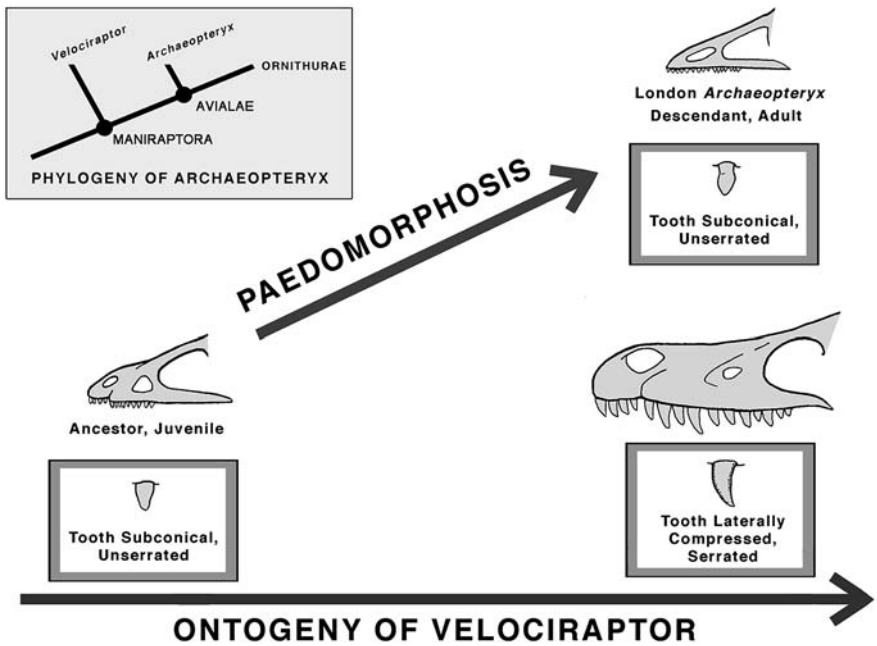


Figure 13.10. Paedomorphic trend in the evolution of *Archaeopteryx* from nonavian theropods such as *Velociraptor*. In *Archaeopteryx*, the teeth are subconical and unserrated as seen in the embryonic *Velociraptor*.

and Templin 2004b) by peramorphism; however, a biplane wing planform reappeared in pygostylians such as *Sapeornis* by paedomorphism (see chapter 12)

Some of the peramorphic trends in the evolution of avialans (*Archaeopteryx* or *Jeholornis*) from nonavian theropods, which may be linked to refinement of flight, include the following:

1. evolution of flight from parachuting to biplane gliding to monoplane gliding (see chapter 12)
2. gradual elongation of the forelimbs relative to the hindlimbs with the development of larger wings (fig. 13.12). The forelimb is about 115% that of the hindlimb in *Archaeopteryx* and 126% that of the hindlimb in *Jeholornis* (Zhou and Zhang 2003).
3. a dorsolaterally facing glenoid facet in *Jeholornis*; in maniraptorans and *Archaeopteryx*, the glenoid facet is laterally placed (Zhou and Zhang 2003)
4. a strut-like coracoid in *Jeholornis*; a short and nonstrut-like coracoid in maniraptorans and *Archaeopteryx* (Zhou and Zhang 2003)

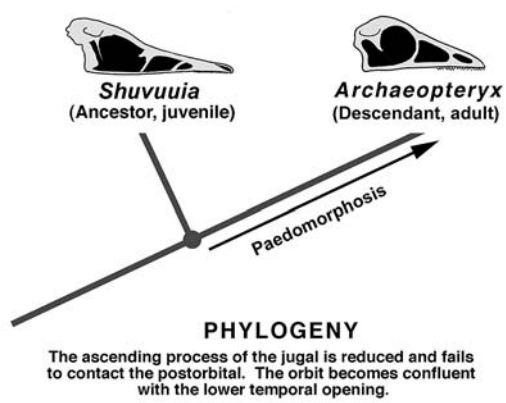

Shuvuuia
(Ancestor, juvenile)
Archaeopteryx
(Descendant, adult)
Paedomorphosis
PHYLOGENY
The ascending process of the jugal is reduced and fails to contact the postorbital. The orbit becomes confluent with the lower temporal opening.

Figure 13.11. Lateral views of a juvenile theropod skull showing the paedomorphic evolution in the temporal configuration of *Archaeopteryx*. In a juvenile theropod such as *Shuvuuia* (Chiappe et al. 2002a), a partial modification of the temporal configuration can be seen with the loss of the ascending process of the jugal so that the orbit becomes confluent with the lower temporal opening, whereas in adult theropods, the diapsid temporal arches remain intact. In *Cathayornis*, a similar configuration of the diapsid arch can be seen as in the juvenile *Shuvuuia*. This confluence of the orbit with the lower temporal opening is regarded as an important character for the inception of cranial kinesis in birds.

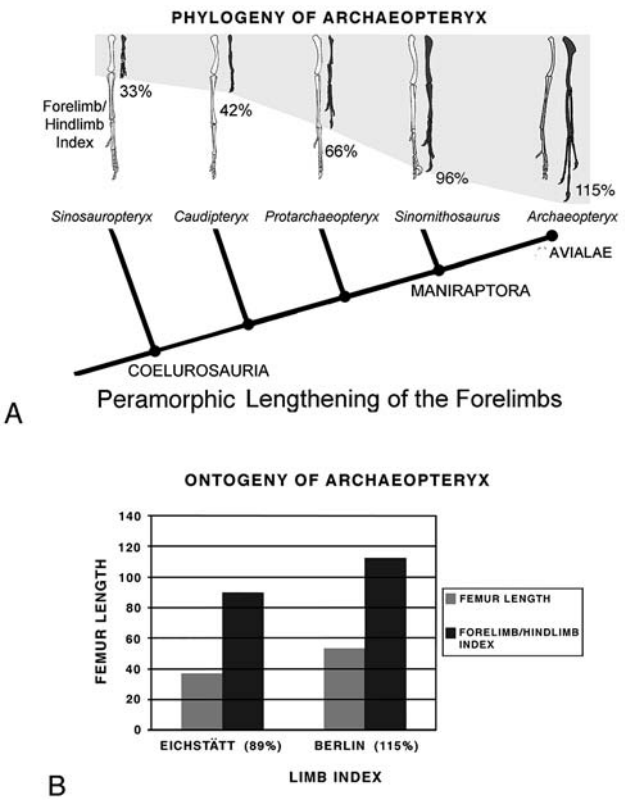


Figure 13.12. Peramorphic trends in the evolution of the wings of *Archaeopteryx* from theropods. A, the cladogram shows the increase of forelimb/hindlimb index in the phylogeny of arboreal theropods; the forelimbs become progressively longer to facilitate climbing. B, similar peramorphic lengthening of the forelimb can be seen from the Eichstätt (young) to Berlin (adult) specimens of *Archaeopteryx*.

5. presence of sternal fenestra in *Jeholornis*; this feature in absent in maniraptorans and *Archaeopteryx* (Zhou and Zheng 2003)
6. the carpometacarpus is well fused proximally in *Jeholornis*, but is separate in maniraptorans and *Archaeopteryx* (Zhou and Zhang 2003)
7. the progressive enlargement of the preacetabular process of the ilium
8. gradual rotation of the pubis backward to form the opisthopubic pelvis (fig. 13.13)
9. reduction of the number of caudal vertebrae to fewer than twenty-five. Usually in nonavian theropods, the number of caudal vertebrae ranges from thirty to fifty (Gatesy 1990).
10. fusion of the tarsometatarsus at the proximal end in *Jeholornis* (Zhou and Zhang 2002)
11. attachment of the metatarsal I more distally to metatarsal II and adaptation of the pes (it becomes anisodactyl) for perching
12. evolution of asymmetric flight feathers in *Archaeopteryx* from the downy feathers of *Sinosauropteryx* (fig. 15.5)

It thus appears that evolution of *Archaeopteryx* and *Jeholornis* from coelophysids represents a complex mosaic of paedomorphic and peramorphic trends.

Level 2. Heterochrony from Avialans to Neognaths

The phylogeny of Mesozoic birds is beginning to emerge from several recent studies using *Archaeopteryx* as the basal group (Chiappe 1995a, 2007; Chatterjee 1997, 2002). The selection pressure for this level of heterochrony was the acquisition of maneuvering flight with endurance and efficient takeoff and landing mechanisms (Chatterjee and Templin 2004a, 2012). This was achieved by the fusion of bones in critical areas of the skeleton for strength and rigidity. Stability of flight was compromised in favor of greater maneuverability by truncation of the long bony tail into a pygostyle. The heterochronic changes in this level of evolution are dominated by the following peramorphic trends. Many of these traits are developed beyond those of the ancestor, so that in effect, extra developmental stages are added to the life history as in peramorphism.

1. closure and fusion of cranial sutures. Cranial sutures are present in juvenile birds, *Archaeopteryx*, and *Jeholornis*, but become closed with maturity (fig. 13.14).
2. heterocoelous cervical centra. In juvenile birds, *Archaeopteryx*, and *Jeholornis*, the centra are amphicoelous but become heterocoelous in adult birds with growth (fig. 13.15), thus allowing a wide range of mobility (Heilmann 1926; Bellairs and Jenkin 1960).
3. an ossified uncinate process (fig. 13.15). This process

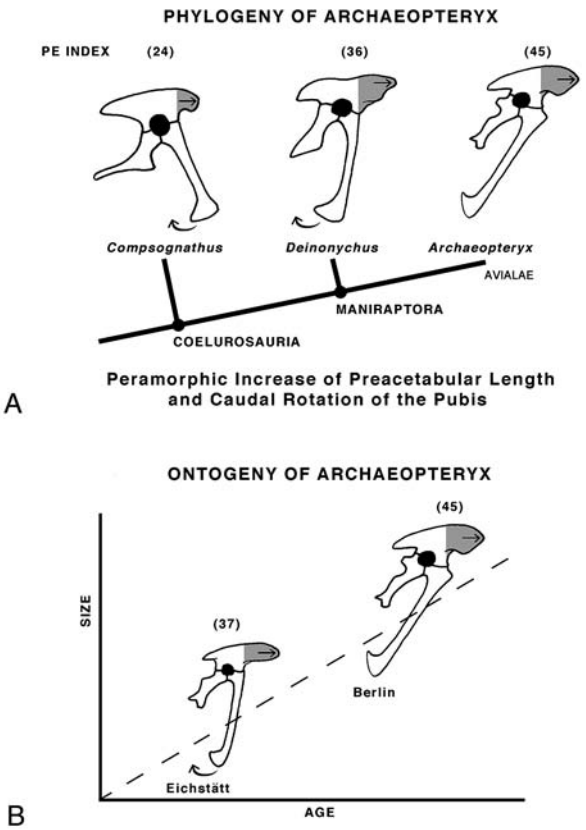


Figure 13.13. Peramorphic trends in the evolution of the pelvis of *Archaeopteryx* from theropods. A, the cladogram shows progressive enlargement of the preacetabular process in theropods, which is quantified in the preacetabular elongation (PE) index (preacetabular length of ilium rostral to pubic peduncle × 100/total length of ilium). The cladogram also depicts the gradual rotation of the pubis in a backward direction. B, similar peramorphic trends in the pelvis can be seen from the Eichstätt (young) to the Berlin (adult) specimens of *Archaeopteryx*.

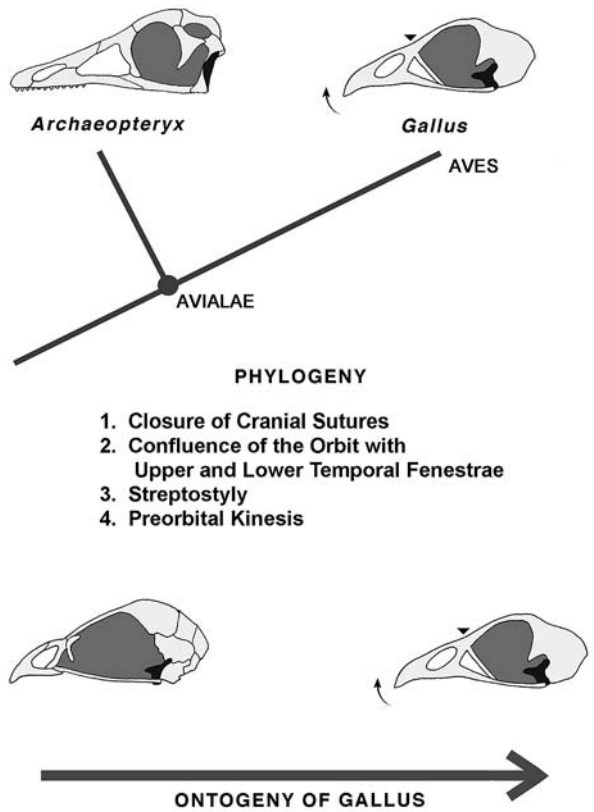


Figure 13.14. Peramorphic trends in the evolution of the neognathous skull from that of *Archaeopteryx*. *Top*, the cladogram shows that in *Archaeopteryx*, the cranial sutures are present but become closed in adult neognaths. *Bottom*, similar trends can be seen during the ontogeny of a chicken (*Gallus*) skull.

remains cartilaginous in juvenile birds, *Archaeopteryx*, and *Jeholornis*, but becomes ossified in adult birds (Heilmann 1926).

4. enlargement of the sternum with a ventral keel (fig. 13.16). In juvenile birds, *Archaeopteryx*, and *Jeholornis*, the sternum is small without a keel but becomes very large with a prominent ventral keel in adult birds (James and Olson 1983).
5. articulation of the scapula and coracoid changing from an obtuse angle in juvenile birds, *Archaeopteryx*, and *Jeholornis*, to an acute angle during growth in adult birds to facilitate flight (fig. 13.16)
6. loss of manual claws and reduction of digits. Many juvenile birds, such as the hoatzin, bear manual claws for climbing when they are young as seen in *Archaeopteryx*, and *Jeholornis*, but they lose them with growth (Parker 1891). In *Archaeopteryx*, the phalangeal formula is 2-3-4-x-x; in adult neognaths the common count is 1-2-1-x-x (fig. 13.17).

The following peramorphic changes are linked to efficient methods of flying, landing, and terrestrial locomotion:

1. evolution of flight from gliding to flapping (see chapter 12)
2. truncation of the tail. In *Archaeopteryx* and *Jeholornis*, the number of caudal vertebrae is twenty to twenty-

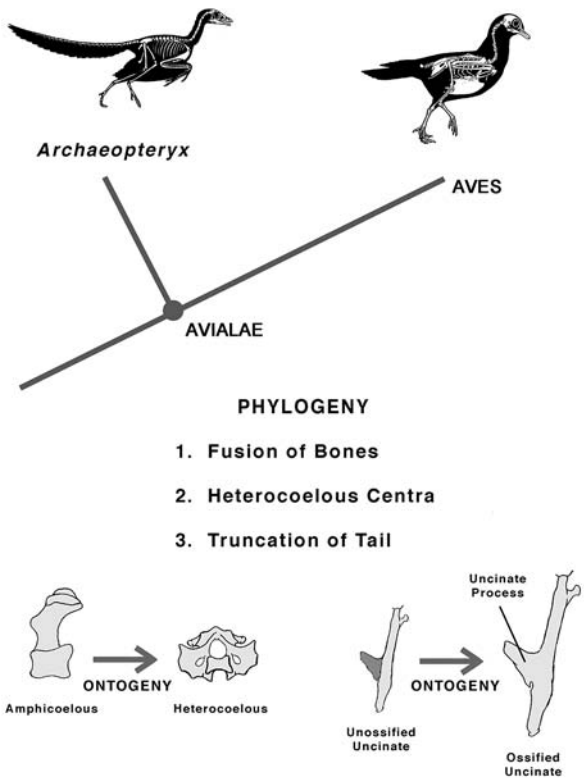


Figure 13.15. Peramorphic trends in the evolution of the neognathous skeleton from that of *Archaeopteryx*. *Top*, the cladogram shows that during the evolution of the neognath skeleton of *Archaeopteryx*, three peramorphic characters can be observed. These include the fusion of ribs (uncinate process), heterocoelous cervical centra, and truncation of the tail. *Bottom*, similar trends can be seen during the ontogeny of a chicken (*Gallus*) skeleton.

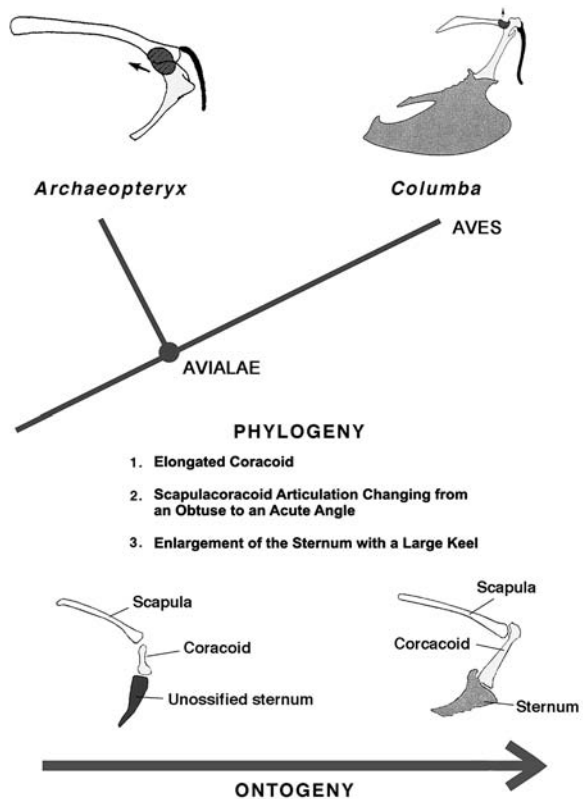


Figure 13.16. Peramorphic trends in the evolution of the neognathous shoulder girdle from that of *Archaeopteryx*. *Top*, the cladogram shows that during the evolution of the neognaths of *Archaeopteryx*, several peramorphic characters in the shoulder girdle can be seen. The coracoid becomes elongated, being as long as the scapula; the articulation between the scapula and coracoid changes from an obtuse to an acute angle; and the sternum becomes large and ossified and develops a strong keel. *Bottom*, similar ontogenetic changes can be seen during the growth of the king rail (*Rallus elegans*; simplified from Olson 1973).

four, but in neognaths, the long bony tail is reduced to a pygostyle with five to eight free caudals (fig. 13.15).

3. fusion of pelvic elements. Both the pubis and the ischium are rotated backward to enclose the obturator and ilioischiadic foramina, respectively; the cranial part of the iliac blade, the preiliac process, is elongated progressively forward (fig. 13.18).
4. fusion of the tibiotarsus. The astragalus and calcaneum are fused to the tibia (fig. 13.19).
5. fusion of the tarsometatarsus. The distal tarsal elements are fused to the metatarsal bones (fig. 13.19).
6. reduction of the fibula. In juvenile form, the fibula is as long as the tibia but is reduced to a splint as the animal grows (fig. 13.19).

The following peramorphic feature is an evolutionary novelty for neognaths and may be linked to feeding:

1. loss of the lower temporal arcades (postorbital-jugal bar and squamosal-quadratojugal bar) so that the orbit becomes confluent with the upper and lower temporal opening (fig. 13.14). Loss of bony vertical struts led to streptostyly of the quadrate and the evolution of cranial kinesis to increase the gape (Chatterjee 1991, 1997).

However, the following two characters may be paedomorphic traits:

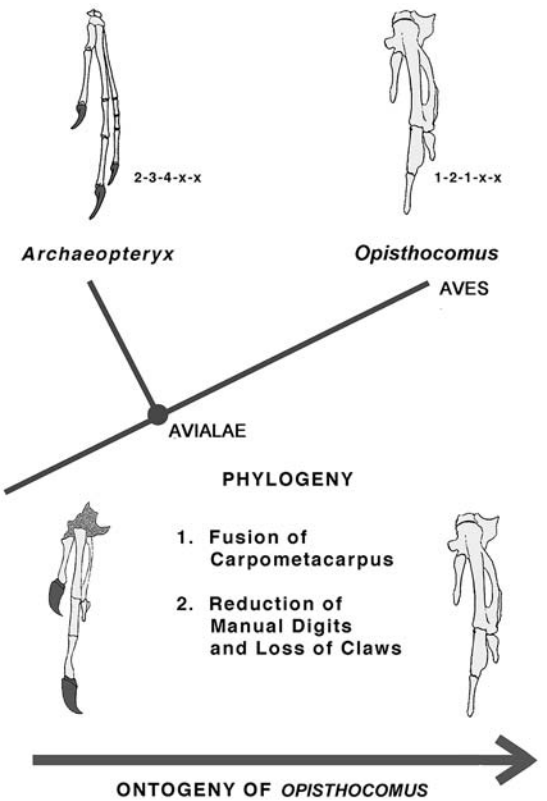


Figure 13.17. Peramorphic trends in the evolution of the neognathous manus of *Archaeopteryx*. *Top*, the cladogram shows that during evolution of neognaths from that of *Archaeopteryx*, several peramorphic characters in the manus can be seen. The carpometacarpus becomes fused for the attachment of primary feathers, accompanied by a reduction of the digits, including claws. Similar trends can be seen during the growth of the hoatzin (*Opisthocomus*; simplified from Parker 1891).

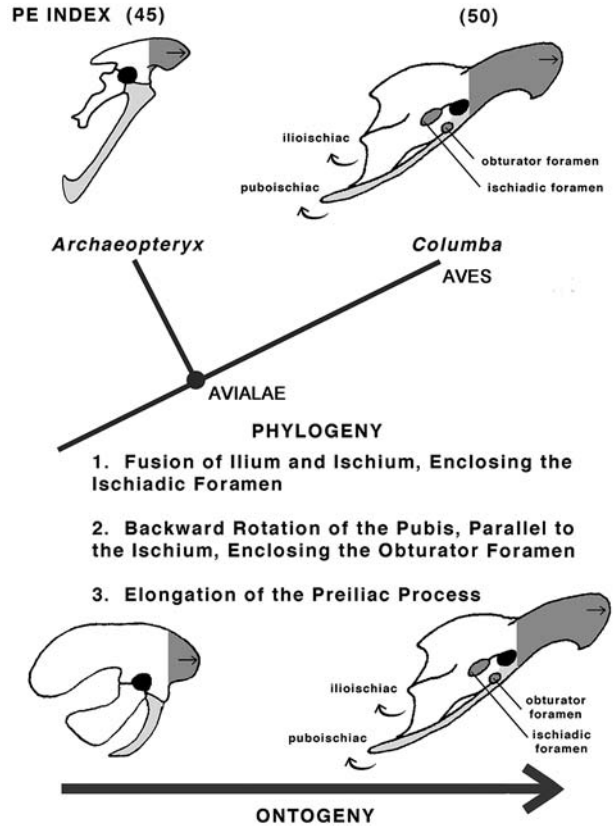


Figure 13.18. Peramorphic trends in the evolution of the neognathous pelvis from that of *Archaeopteryx*. *Top*, the cladogram shows enlargement of the preacetabular process in neognaths of *Archaeopteryx* with the fusion of three elements. It also depicts the gradual rotation of the ischium and pubis in a backward direction to enclose the ischiadic and obturator foramina, respectively. Similar trends can be seen during the growth of a chicken (*Gallus*).

1. precocial to altricial development. Limited embryonic fossil evidence of theropods (Geist and Jones 1996) such as *Oviraptor* (Norell et al. 1994), *Troodon* (Varrichio et al. 1999), *Gobipteryx* (Elzanowski 1981), and *Gobipipus* (Chatterjee 1997) indicates that a precocial mode of development was primitive for neognaths, inherited from theropod ancestors. The eggs of nonavian coelurosaurs were incubated with a combination of soil and direct parental contact (brooding). Altriciality is a paedomorphic mode of development, which might have evolved later in the phylogeny of neognathous birds, when eggs were placed in an arboreal nest with associated parental care (fig. 13.20).
2. progressive enlargement of the brain. The larger relative brain size of neognaths is a paedomorphic feature as the EQ changes inversely with the development in modern birds (*Gallus*). From *Archaeopteryx* to neognaths, the encephalization quotient (EQ) has increased from 0.34 to as much as 1.6 in *Corvus* (Chatterjee 1991). However, the EQ is relatively large in juvenile birds compared to adult forms, indicating the role of paedomorphism in progressive enlargement of the brain in avian phylogeny (fig. 13.21).

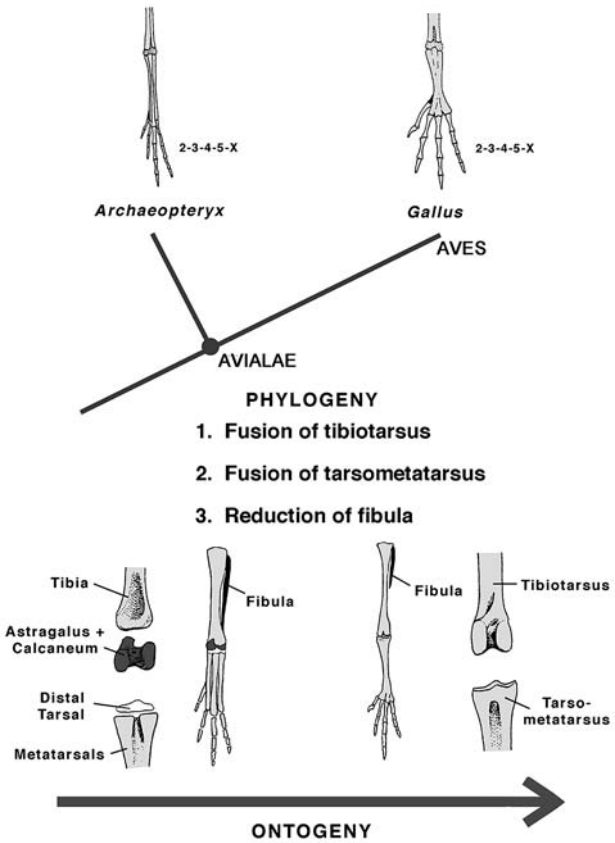


Figure 13.19. Peramorphic trends in the evolution of the neognathous hindlimb from that of *Archaeopteryx*. *Top*, the cladogram shows fusion of the tibiotarsus and tarsometatarsus and the reduction of the fibula. Similar trends can be seen during the growth of a chicken (*Gallus*). *Bottom*, ontogeny of chicken (*Gallus*) showing fusion of the tibiotarsus and tarsometatarsus with growth.

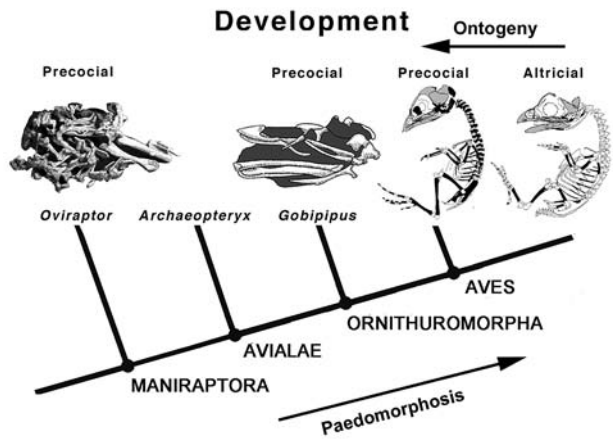


Figure 13.20. Phylogeny of theropods showing the evolution of altricial development from a precocial mode. The precocial mode is interpreted as primitive, whereas the altricial is derived and peramorphic (Starck 1989; *Oviraptor* from Norell et al. 1994; *Gobipipus* from Chatterjee 1997; precocial bird, Japanese quail [*Coturnix*] and altricial bird, Java sparrow [*Lonchura*] from Starck 1989).

Level 3. Heterochrony from Neognaths to Flightless Birds

Physiologically, flight is an expensive endeavor, and flightlessness is a recurrent theme in avian evolution. It principally occurs when potential predators are lacking, and serves to save energy. A variety of birds, such as ornithurines, palaeognaths, and neognaths, have become secondarily flightless. Among ornithurines, hesperornithiforms and *Patagopteryx* are early examples of flightless adaptations. Among palaeognaths, the ratites such as ostriches, rheas, emus, and several extinct forms are the most celebrated flightless birds. Among neognaths, both gruiforms (cranes, rails, and allies) and penguins include a large number of flightless species. Flightlessness has evolved independently among three genera of grebe, nine different lineages of waterfowl, and several genera of auk (Feduccia 1996). James and Olson (1983) documented several species of ibis, goose, rail, and pigeon in the Pacific islands that reverted to flightless forms during prehistoric times because of geographic isolation and the relative absence of predators. It is generally believed that modern ratites evolved from their flying ancestors as a result of paedomorphism (de Beer 1958).

All birds are flightless when they are small chicks, and the hatchlings of flying birds show features similar to those that characterize adult flightless birds. Paedomorphosis has been a major component of the evolution of flightless birds, especially in the reduction of the flight apparatus, leading to juvenilized morphology. These paedomorphic features mirroring the juvenile condition of neognaths include the following (Feduccia 1996):

1. retention of cranial sutures
2. small wings (fig. 13.22).
3. disproportionately short distal wing elements (fig. 13.22)

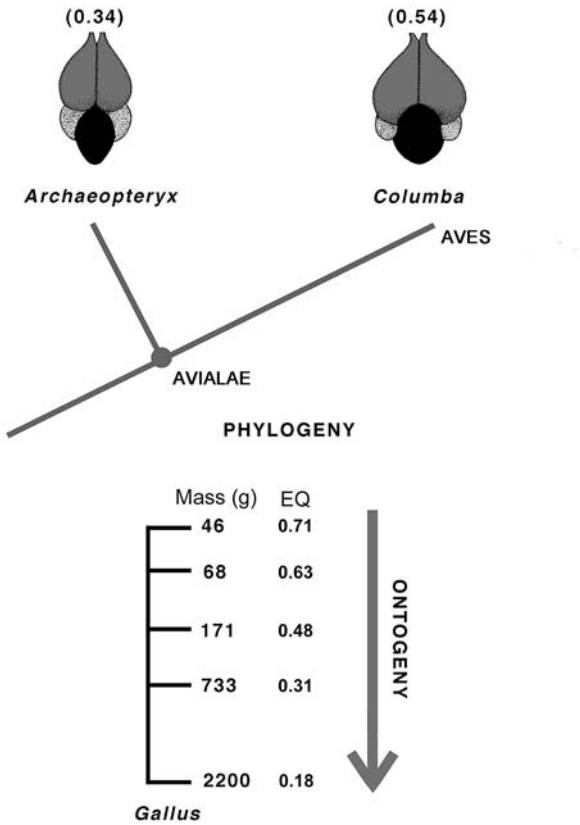


Figure 13.21. Paedomorphic evolution of the neognathous brain from that of *Archaeopteryx*. *Top*, there is an increase of the encephalization quotient (EQ) from 0.34 to 0.54 as the brain becomes more and more enlarged. *Bottom*, body weight in modern neognaths, such as the chicken (*Gallus*), is inversely correlated with EQs during ontogeny; the smaller the animal, the larger the relative brain size (Chatterjee 1997).

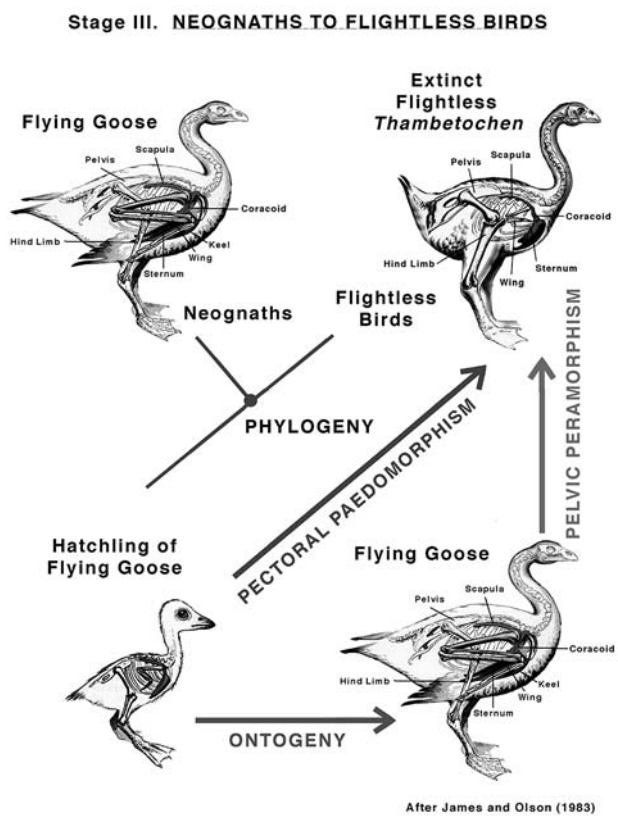


Figure 13.22. Dissociated heterochrony in flightless birds. *Thambetochen* (*upper right*), an extinct Hawaiian flightless goose, shows paedomorphosis in the loss of wings and a reduced sternum, as seen in the hatchling of a flying goose (*lower left*). However, peramorphic trends can be seen in *Thambetochen* with the development of a massive pelvis, stronger and stouter hindlimbs, a large skull, and increased body size in relation to a typical flying goose (*upper left*) (James and Olson 1983). *Lower right*, some of the skeletal features of the adult *Thambetochen* result from the retention of juvenile characters in the flight apparatus of the hatchling of a flying goose by paedomorphism.

4. a reduced and flat-bottomed sternum with little or no keel (fig. 13.22)
5. a reduced scapulocoracoid (fig. 13.22)
6. a reduced furcula with a splint-like structure (fig. 13.22)
7. an obtuse angle of articulation between the scapula and the coracoid (fig. 13.22)
8. a broad, unossified region between ilium and ischium (ilioischiadic fenestra) (fig. 13.22)
9. downy, juvenile-like feathers

Thus, many paedomorphic characters in flightless birds are, in fact, derived and represent apomorphic reversals in a phylogenetic context, resembling primitive or ancestral stages. Such reversals may simply reflect neotenic solutions to particular adaptive problems. Large body size is frequently associated with ratites and may enhance foraging and partitioning of feeding strategies (Livezey 1993). By delaying the onset of maturity, and leading to large body sizes, hypermorphosis in flightless birds may be linked with the stable K-selected insular environments lacking large predators.

In contrast, several features in flightless species are "overdeveloped" in comparison to those of their flying

ancestors, and presumably represent peramorphism (McKinney and McNamara 1991). These peramorphic features include:

1. a huge skull (fig. 13.22)
2. increased body size (fig. 13.22)
3. a massive pelvic girdle (fig. 13.22)
4. enormous hindlimbs (fig. 13.22)

Because of the loss of flight, selection favors alternative and efficient methods of locomotion involving hindlimbs. Thus flightless birds show a combined effect of dissociated heterochrony—pectoral peramorphosis and pelvic paedomorphosis (McKinney and McNamara 1991).

Conclusion

Heterochrony has been a major factor in the origin and evolution of birds and their flight, but its role has never been investigated before. The integration of phylogeny and ontogeny indicates that heterochrony has played a major role in the macroevolution of birds at different hierarchical levels. This work has demonstrated the need for multiple, hierarchically nested levels of avian phylogeny in the analysis of heterochrony. In each level, a combination of paedomorphic and peramorphic processes has operated at a varying degree, and often one process has dominated the other. Gould (1977) argued on theoretical grounds that paedomorphosis should be as frequent as peramorphosis. The heterochrony of birds, when analyzed at different levels, supports Gould's contention. Paedomorphism was dominant during the transition from basal theropods to early avialans associated with the miniaturization of size. On the other hand, peramorphism was dominant during the evolution of neognaths from avialans with the acquisition of new characters associated with the refinement of flight. Finally, during recurrent flightlessness, paedomorphism played crucial roles. The success of birds lies in the dissociated nature of heterochrony at different hierarchical levels that led to an adaptive breakthrough that resulted in the conquest of air with a small and light skeleton.

14 Feathers and Footprints

The day is done, and the darkness
Falls from the wings of Night,
As a feather is wafted downward,
From an eagle in his flight.

Henry Wadsworth Longfellow, *The Belfry of Bruges and Other Poems*, 1845

And, departing, leave behind us
Footprints on the sands of time.

Henry Wadsworth Longfellow, *A Psalm of Life*, 1838

Feathers of a Wing

Feathers are architectural marvels with an amazing diversity, essential to the survival of birds and their theropod antecedents. They combine lightness, strength, and flexibility with intricate architecture and come in a huge range of shapes, sizes, and colors for a wide variety of functions. Feathers fulfill vital needs of birds, aiding in providing the aerodynamic power necessary for flight. They streamline, insulate, and waterproof a bird's body; provide coloration for courtship, communication, and camouflage; attract a mate; incubate eggs; and provide balance when a bird is on the ground (Stettenheim 2000). They form a light, soft, warm, and sturdy coat that provides grace and beauty, tactile sensation, and protection from injury. They play key roles in many natural and sexual selection processes. Some feathers form lifting and control surfaces on the wings and tail that are essential for flight. These feathers, called contour feathers, have a stiff, central rachis with webs on each side that make up the flat vane. The vanes are composed of hundreds of pairs of branches, called barbs, extending diagonally out from the central rachis on each side. The long asymmetric contour feathers on hands make the wings bigger; increase wingspan; and play important roles in propelling, lifting, and controlling flight. The stiffness of tail feathers helps in balancing while perching, and steering and pitching while flying. Another type of contour feathers that are short, smooth, and waterproof cover the body and give it a streamlined shape to reduce drag. Short, fluffy down feathers lie next to the skin and help keep the bird warm. A bird can fluff its down feathers for added insulation on cold nights. Some feathers can make or muffle noise. The hair-like filoplumes probably function as mechanoreceptors for sensing airflow over the wings. Finally, the coloration of feathers provides some birds camouflage so that they

can blend in well with the background of their normal surroundings to avoid predator detection. Feather patterns and coloration are important in species recognition and sexual display. Birds attract their mates by a combination of visible signals, including brightly colored plumage. Feathers are probably the most indispensable and conspicuous apparatus for survival of birds. No wonder they spend a good deal of time preening, dusting, oiling, and otherwise caring for their feathers.

Although skeletal remains are the most important fossils for tracing the evolution of Mesozoic birds, feathers provide additional evidence for their existence and activities in the Mesozoic ecosystem. These trace fossils are important to demonstrate the birds' size, diversity, flight capability, and paleoecology. Feathers reveal the natural history of ancient birds, their environments and distributions in time and space. Feathers are the most complex form of body covering to be found in any vertebrates, varying from long flight feathers to mere puffs of down. They reveal a spectacular range of patterns and colors. Keratin, the same type of protein that gives strength to hair and nails, makes feathers light, strong, and flexible. Feathers are complex composites of biological material in which keratins are embedded in an amorphous protein matrix whose mechanical properties are outstanding as they are resistant to water, microbes and fungi.

But for all their complex structure and beauty, fully grown feathers are dead tissues.

Feathers in Modern Birds

Avian feathers are characterized by structural diversity and hierarchical development. Most feathers fall into two basic types: pennaceous, or contour, feathers with paired barbs fused to a central rachis to form vanes; and plumaceous, or downy, feathers, which are underneath the contour feathers. There are various intergrades between these two basic morphotypes that give rise to six major types of feathers in modern flying birds: contour feathers, down feathers, semiplumes, filoplumes, powder feathers, and bristles (fig. 14.1). Contour feathers are the basic vaned feathers of the body and wings; they coat the body, giving it contour, color, protection, and a streamlined shape. A few of the contour feathers on the wing (remiges) and tail (rectrices) have become large and highly specialized for flight (or display). Primary remiges (supported by the hand) and rectrices show asymmetrical vanes for aerodynamic function. Flight feathers are stiffened to absorb compressive force during downstroke but are flexible in other directions. The smaller contour feathers that cover the body have symmetrical vanes. The distal vane area of the body contour feather is firm and pennaceous, but its proximal region is soft and plumaceous because its barbules lack hooks. Contour feathers grow only in feather tracts (pterylae). The coverts are short feathers that cover part of the remiges and rectrices and give them additional rigidity. The other kinds of feathers are primarily used for insulation, protection, grooming, waterproofing, and sensation.

The key to successful flight is the structure of the feather. A typical contour feather is composed of a long, tapering central shaft (rachis) with broad, flexible vanes on either side. Vanes may be symmetrical or asymmetrical. Vanes are asymmetrical in flight feathers, the remiges of the wings, and the rectrices of a tail; the leading edge is narrower and stronger than the trailing edge. Remiges of the wings include the primaries, secondaries, and tertiaries. Because air pressure is greater along each feather's front edge, the asymmetric configuration is a requirement for powered flight, giving the feather a curved, airfoil cross section for aerodynamic function. In flightless birds, the vanes are symmetrical (fig. 14.1).

The vanes follow fractal geometry and are composed of many barbs, which in turn bear many still smaller interlocking barbules; the barbules form a strong, light, flexible surface, one that can be restored by preening after it is broken apart. Each barb is a miniature version of a contour feather with a central shaft and lateral barbules. Feathers need constant care (preening, oiling, powdering, shaking, and stretching) to keep them in good shape. However, feathers are dead, horny structures and deteriorate with time; once a year birds must renew their contour feathers, usually after the breeding season.

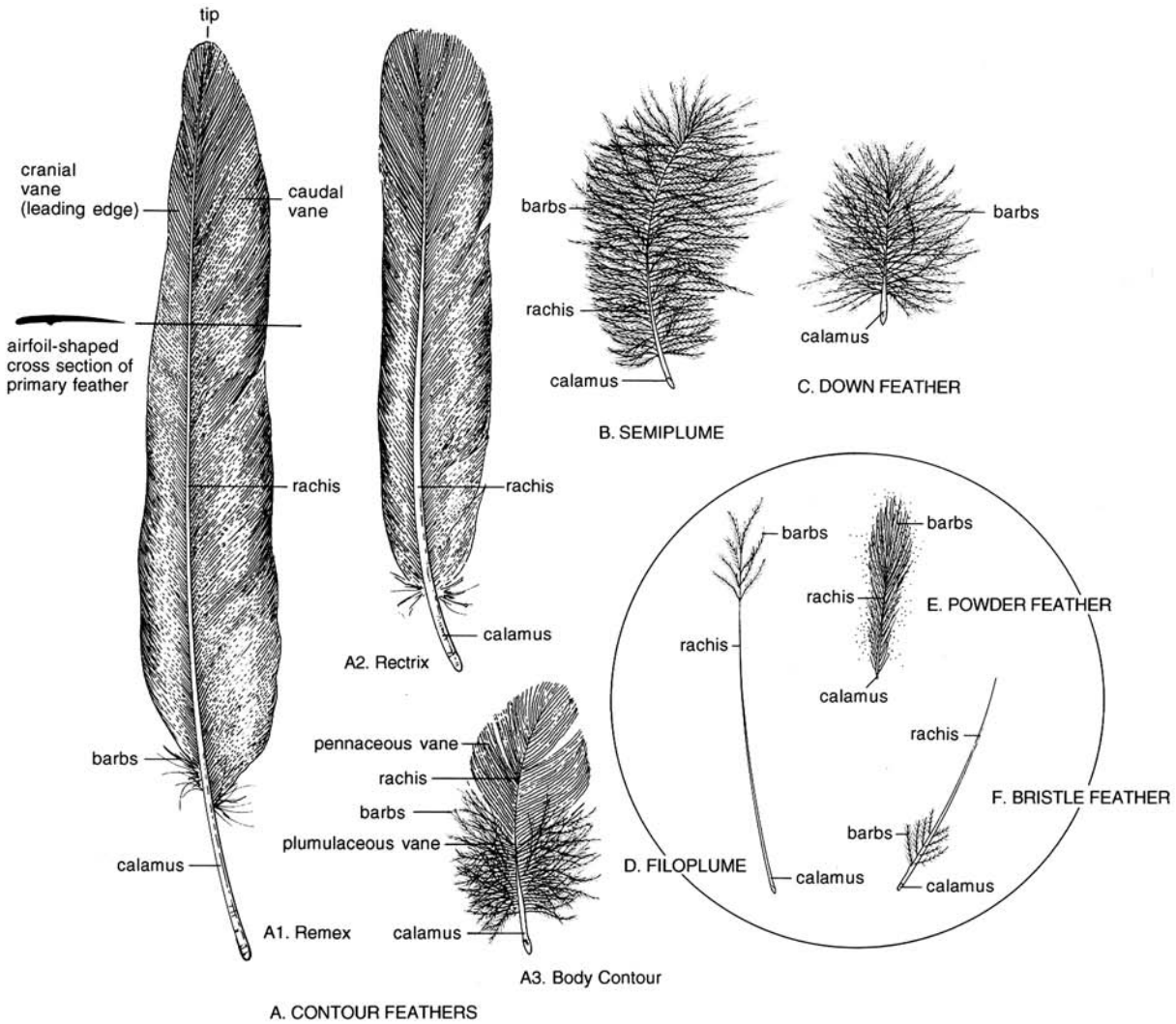


Figure 14.1. The major types of feathers in modern birds. A, contour feathers are the basic vaned feathers, including the large flight feathers of the wing (A1, remex) and tail (A2, rectrix) and the smaller body feathers (A3, body contour); B, semiplume; C, down feather; D, filoplume; E, powder feather; F, bristle feather.

The Origin of Feathers

Although flight evolved many times during the history of life, birds and their dinosaur antecedents are the only animals that possess feathers. Recent spectacular fossil finds of feathered dinosaurs from China have provided critical insights on how these incredibly strong and lightweight feathers evolved in a series of stages in coelurosaurs in concert with insulation, sexual display, and flight improvement. It becomes clear that feathers evolved in dinosaurs long before the origin of birds. Whatever the original purpose of feathers, they were probably around for millions of years before some lineage of theropods began to use them for insulation, for sexual display, and ultimately for flight.

Feathers are the most complex integumentary structures found in vertebrates. They have an intricate, branched structure, and grow from their bases by a unique mechanism. Like hair, nails, and horns, feathers are inert structures when mature and are made from a protein called

keratin. Although feathers cover most parts of the body of birds, they arise only from certain well-defined tracks on the skin, termed pterylae, with featherless areas in between. The feathers grow from special papillae, which produce one, two, or three sets of feathers each year. Feathers are dead, horny structures that deteriorate with time; once a year birds must renew their contour feathers, usually after breeding season, to make them airworthy.

The origin of feathers remains controversial and poorly understood because of lack of transitional fossils until recently, making them a challenge to evolutionary biologists. What was the nature of the ancestral protofeather, and what was its function? Are they modified scales, or evolutionary novelties? These are some hot-button issues. I note here divergent opinions on the origin and evolution of feathers by several current researchers and new emerging concepts from paleontological and developmental constraints. There are two broad theories for the origin of feathers: (1) feathers evolved from reptilian scales; or (2) feathers evolved from a similar epidermal mechanism with different *Hox* genes controlling development. *Hox* genes are the genetic toolkit that controls the body plan of an animal. Recent discovery of feathered dinosaurs from China showing all the transitional stages of primitive feathers in concert with neontological data of feather development appear to have settled this long-standing evolutionary puzzle about the origin of feathers.

Modification of Reptilian Scales

It is generally believed that primitive feathers developed by elongation and division of reptilian scales because they share similar keratinous tissue such as beta-keratin (Rawles 1963; Maderson 1972; Maderson and Alibardi 2000). Regal (1975) speculated that a hypothetical intermediate stage might bridge the gap between the reptilian scale and the avian feather; this protofeather consisted of a long, tapered central shaft that supported enlarged, overlapping scales on its two sides. The vane was asymmetrical, as in a flight feather, while the scales were flexible and might have been precursors to barbs. These elongated scales would be placed in an overlapping fashion and could be folded over one another when not in use. Sharov (1970) described an interesting diapsid reptile, *Longisquama* from the Triassic lakebeds of Kyrgyzstan, in which overlapping, elongated scales are found along the dorsal appendages and clavicles (fig. 3.7A). Sharov concluded that these elongated scales were attached to the back in life and may have functioned as a kind of parachute, braking the animal's fall as it jumped from branch to branch or from the trees to the ground. He suggested that these scales constitute a structural stage in the evolution of feathers. Maderson (1972) and Jones et al. (2000) showed how these elongated scales of *Longisquama* could give rise to the protofeathers of early birds through a series of transformations. Eventually, these protofeathers would increase the wingspan and reduce the wingtip vortex during the gliding stage. Finally, the lateral plates would give rise to the vanes of a contour feather (fig. 14.2).

Modern birds possess both feathers and scales. Horny scales similar to those of reptiles cover the lower legs and toes. Rawles (1963) has shown that transplants of embryonic epidermis may produce either scales or feathers, depending on the nature of the underlying dermis. Scales and feathers have a common developmental origin; both develop from similar germ buds. The conversion of scales into feathers is known in some living birds. For example, young pigeons have legs covered with scales, but feathers in adult pigeons replace the scales. In some hawks, scales on the legs support some rudimentary feathers. In the bald eagle, scales cover the bare tarsus; in the golden eagle, however, feathers cover the tarsus.

Theories about the origin of feathers focus on adaptive and functional explanations of the evolution of feathers from reptilian scales: (1) feathers evolved in connection with flight, or (2) feathers evolved as insulation to retain body heat. Because feathers are uniquely designed for flight, it is not surprising that much speculation about the origin of feathers is related to the origin of flight. Heilmann (1926) suggested that feathers evolved in an aerodynamic context from elongated proavian scales that lay on the trailing edges of the tail and body. These elongated scales would provide an airfoil surface to slow the fall of the proavian during parachuting and gliding.

Parkes (1966) also argued that flight feathers evolved

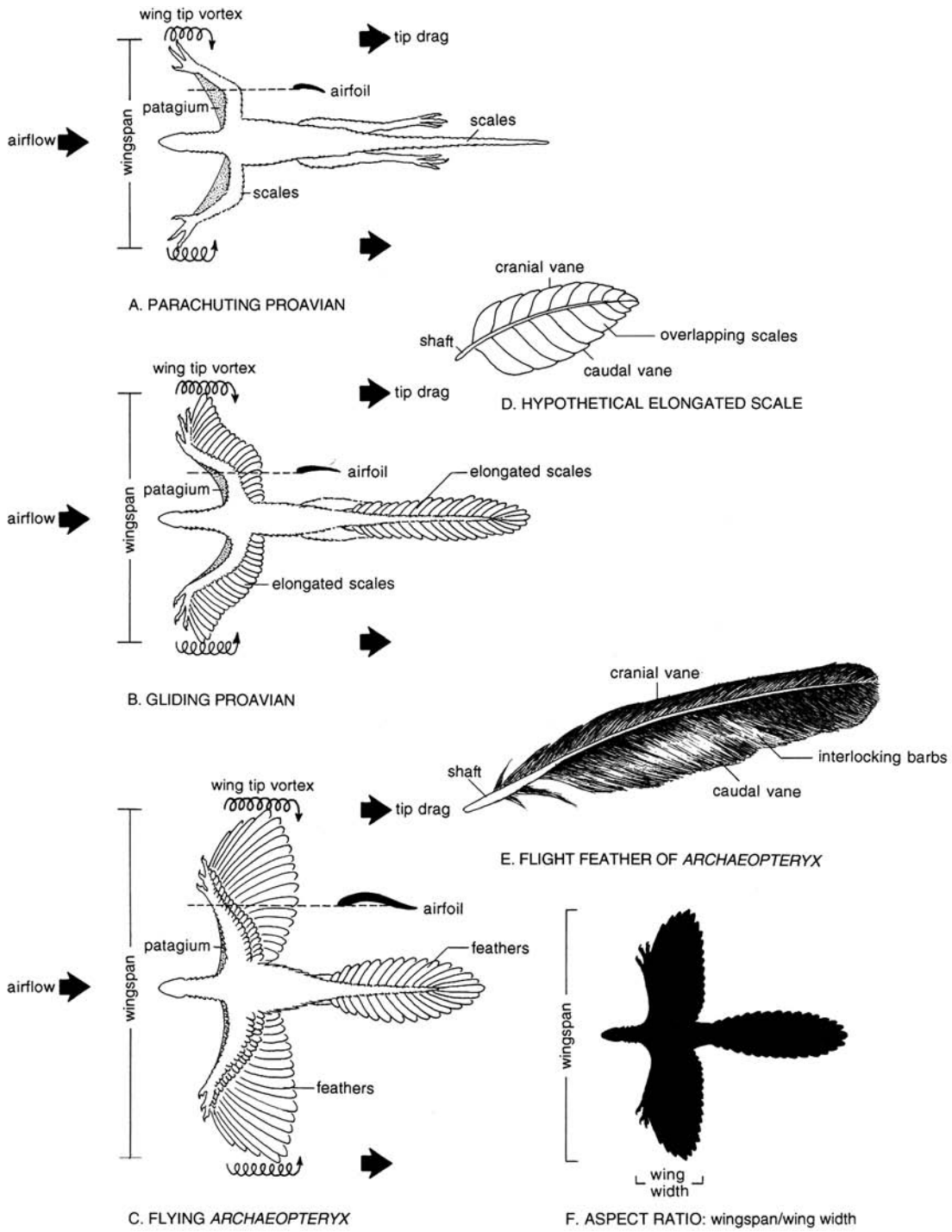


Figure 14.2. Origin of feathers from reptilian scales. Dorsal views of the hypothetical parachuting proavian (A) and gliding proavian (B) and the flying *Archaeopteryx* (C) showing how elongated scales and flight feathers in early birds might have increased the wingspan and airfoil surface to decrease the interference of the wingtip vortex. D, hypothetical elongated scales developed during gliding flight to increase the airfoil surface and were precursors to feathers. E, isolated flight feather of *Archaeopteryx* showing the asymmetrical vanes. F, the aspect ratio is the ratio between wingspan and wing width and is an important feature of the flight characteristics of birds. A gliding proavian (B) with long, narrow wings has a higher aspect ratio than does *Archaeopteryx* (C), with broad wings.

early on the wings and tail by providing an increased airfoil. Once flight was achieved, simple, degenerate feathers spread all over the body for further insulation, resulting in the appearance of down feathers. Alan Feduccia (1980, 1985, 1995a, 1996) provided some recent examples in support of this flight model. First, in leaping lemurs such as Malagasy sifakas (*Propithecus*), which possess a gliding membrane, a thick fringe of elongated hairs develops along the caudal forelimbs. Using this analogy Feduccia argued that primitive contour feathers along the caudal edge of the forelimbs and the lateral margins of the tail could provide the initial stage in the evolution of an airfoil. Second, in recent flightless birds, such as the ostrich, rhea, cassowary, and kiwi, feathers are primarily for insulation; these feathers have become degenerate, lost their pennaceous structure and aerodynamic design, and become fluffy and hair-like in structure. Feduccia thus questioned why such complicated structures as feathers would be evolved in the first place if they were originally adapted for temperature control. He maintained that feathers first evolved in the context of flight and later were co-opted for insulation.

Opponents argue that contour feathers were primitive, whereas flight feathers appeared late in evolution. They propose that selection for the initial development of feathers in early protobirds was for the function of insulation and later was an exaptation for flight (Bakker 1975; Regal 1975; Ostrom 1979; Bock 1986; Bock and Bühler 1995). Since trees are considerably cooler than the ground, an insulating cover of feathers on the body was advantageous for arboreal protobirds. Eventually, during gliding, unspecialized contour feathers along the caudal border of the forelimbs and the lateral margins of the tail evolved into asymmetrical remiges and rectrices for aerodynamic function.

The Developmental Model

Recent work indicates that scale formation in avian legs and feet requires a repression of feather development, different from pedal scales of reptiles, possibly mediated by *Hox* genes (Sawyer et al. 2005). The avian scales on legs and feet are secondarily derived from feathers by developmental constraints, and this view is supported by recent fossil evidence. Thus reptilian scales and avian scales are not homologous but have different developmental trajectories. The avian scales first appear in ornithuromorph birds such as *Yanornis* from China when flight was perfected but are absent in avialans, indicating that they were highly derived structures (Xu and Guo 2009). Both paleontological and neontological data demonstrate that feathers were not modified reptilian scales but evolutionary innovative structures.

Ontogeny of Feathers

Recent molecular data and developmental trajectory contradict the scale-based origin of feathers. The proteins that make feathers in living birds are completely unlike the proteins that make reptilian scales. While most scales are composed of alpha-keratins and the smaller family of beta-keratins, feathers also contain a novel type of theta-keratin with a follicular mechanism for production and assembly. Moreover, scales are inherently laminar or planar folds of the skin, while feathers are essentially tubular epidermal appendages that form from follicles (Brush 2000). Feathers originate in a skin layer deep under the outer layer that forms scales. It is very unlikely that feathers evolved from reptilian scales. The partial or complete replacement of avian foot scales by down feathers has been cited as strong evidence for a scale-feather transition (Rawles 1963). However, recent experiments indicate that blockage of bone morphogenetic protein (BMP) causes the foot scales of the chick to develop into feathers (Zou and Niswander 1996). These studies suggest that feathers are not modified reptilian scales but are innovations in theropod lineages that evolved sequentially during the origin of birds and their flight.

Heterochrony may provide an additional clue to the origin of feathers. It is the mechanism by which a species gives rise to descendant species through changes in the timing or rate of developmental events relative to the ancestral condition (McKinney and McNamara 1991). Heterochrony provides the raw material on which natural selection works. Lucas and Stettenheim (1972) showed that the development of different kinds of feathers occurs

in a hierarchical fashion in successive generations. The natal down appears in the first generation during embryonic life, which is followed by a second-generation adult down, then plumaceous feathers, and finally contour feathers. Chatterjee and Templin (2004a) argued that heterochrony might have played a key role in feather evolution. They suggested that feather evolution might have a peramorphic trend with increased complexity where ontogeny of feathers may recapitulate their phylogeny. Evidence of ontogeny and the fossil record suggest that primitive feathers were simple, hollow, filaments that covered the body of coelurosaurs for courtship or insulation purposes.

Richard Prum and Alan Brush have elaborated the developmental model for the origin of feathers from the simplest feather follicles to modern feathers through a series of evolutionary novelties in feather development (Prum and Brush 2003). This model provides critical insights about how feathers might have originated in feathered dinosaurs based on how a feather grows in living birds. A wide variety of feathers appeared in Jehol coelurosaurs in hierarchical fashion that correspond well with the developmental model. Feathers, then, did not evolve for flight but were already present in theropod dinosaurs, presumably for insulation or courtship display, and were later modified to become flying structures.

Prum and Brush suggested that there is a fundamental structural difference between scales and feathers and how they grow. Both scales and feathers grow from skin patches called placodes but in different styles, probably mediated by different *Hox* genes controlling development. Scales form a plate-like structure similar to a folded napkin that grows horizontally, protruding outward as extensions of the epidermis. Feathers, on the other hand are hollow tubes like straws that grow vertically. Feathers are not formed by modification of scales, but are possibly de novo structures, erupting from placodes vertically. Like reptilian scales, feathers grow by proliferation and differentiation of keratinocytes, the keratin-producing cells in the epidermis. When these cells die, they leave behind a mass of deposited keratin. In reptiles and birds, scales and feathers are made of beta-keratins. The outer covering of the growing feather, called the sheath, is made of the softer alpha-keratin, which makes human skin and hair. Recent molecular data suggest that reptilian scales and avian feathers are not homologous; the latter contains a unique protein molecule, a larger theta-keratin, and a follicular mechanism for production and assembly (Brush 2000). Feathers and scales are distinct at genomic, molecular, developmental, and morphological levels.

According to the new developmental model proposed by Prum and Brush, feathers are epidermal, or outer skin, structures that first appear as little bumps (placodes) on the skin of the embryo; each placode soon develops into a backward-projecting cone, the feather germ. Proliferation of cells in a ring around the feather germ creates the feather follicle, all around its base. The root of the feather follicle, in association with the dermal pulp cavity, begins to form a feather. The outermost epidermal layer becomes the feather sheath, a temporary structure that protects the growing feather. The internal epidermal layer within the sheath is differentiated into a central rachis ridge that supports a series of transverse barb ridges on its two sides; the former grow as a rachis, the latter as barbs of a feather. The rachis is formed by fusion of barb basal ends through helical growth in modern contour feathers (Lucas and Stettenheim 1972). Barb ridges play a central role in feather development and they finally develop into hierarchical branches of barbs and barbules. As growth proceeds, the tip of a feather gradually emerges from the growing sheath in planar form, unrolling and splitting apart to form a flat blade or planar feather. (Bilaterally arranged barbs along a central rachis indicate the presence of a planar form.) When the feather reaches its final stage, the follicle collar forms the calamus. Eventually the feather sheath falls away, leaving the fully formed feather (fig. 14.3). At this stage, as their blood supply is cut off, feathers become dead tissues and take on their critical roles. When they are worn out, they are finally discarded during molting.

In this developmental model, there are five stages in feather development that follow the evolution of follicle, each of which is essential for the appearance of the next stage with greater complexity (Prum and Brush 2003;

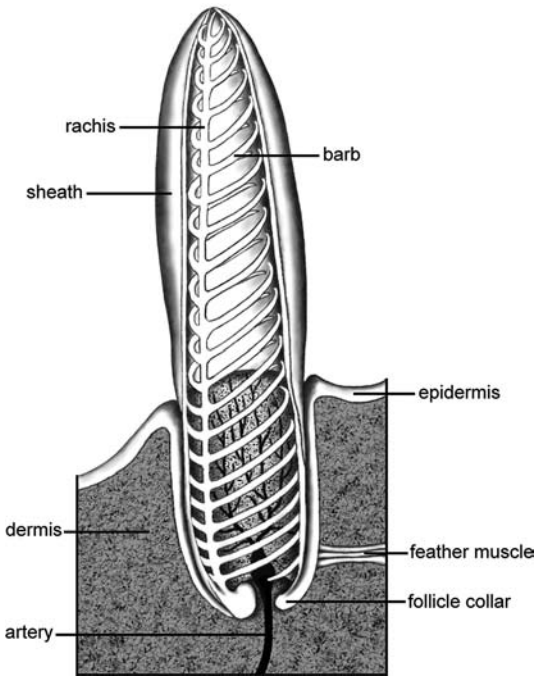


Figure 14.3. Section of bird skin showing successive stages of growth of new feathers. Feathers are made from a protein called beta-keratin, which is found in the epidermis layer of the skin. Feather growth begins with the placode that forms a long tube with a circular collar at the base. The feather itself forms within a sheath for protection. Inside a sheath, there is a central rachis ridge and a pair of barb ridges, which subsequently grow to form a contour feather. Eventually, the feather sheath falls away, leaving the fully formed feather (simplified from Prum and Brush 2003).

Xing and Guo 2009; Zimmer 2011). In the first stage, the follicle produces an unbranched structure, a single hollow cylinder filament anchored in a small pit, the feather follicle. In the second stage, the cylinder subdivides into a tuft of unbranched barbs that is attached to a calamus at the base. This stage corresponds with natal down, which is simple in structure and lacks a central rachis; natal down covers hatchling birds. In the third stage, the barbs fuse to form a shaft, a central rachis; multiple filaments branch laterally from the rachis to form barbs. This stage corresponds with the semiplume feathers, with a central rachis that is longer than any of the lateral downy barbs; they lie under the surface of the contour feathers. The fourth stage is composite with the evolution of a long contour feather where branches on barbs, called barbules, evolved. The barbs possess two rows of barbules of different types, the proximal and distal barbules. Proximally, the vanes are open structures and become plumaceous or downy. Distally, the hooked barbules interlock, forming a symmetrical contour feather with closed vanes, similar to a Velcro fastener and thereby maintaining the integrity of the vane. The interlocking system characterizes the pennaceous feather structure in the distal part of the contour feather, making it a firm, blade-like, and airtight flight surface. Contour feathers are the basic vaned feathers of the body and wings. The fifth stage is the appearance of a long asymmetric feather of the remix of the wing and the rectrix of the tail. This is a flight feather with a long and robust rachis and unequal closed vanes on either side of the rachis, which resists the flow of the air upward through the vane surface.

The developmental model of Prum and Brush (2003) proposes a series of cumulative evolutionary steps leading to modern feathers; each step required a new innovation in the follicle: a simple filament led to a divided, downy filaments that centered on a rachis; helical growth led to the rachis; paired barbs led to barbules; and so on. The simple hollow tubes later evolved into more elaborate structures with interconnected barbs forming flat vanes that led to asymmetric flight feathers in remiges and rectrices (fig. 14.4).

Phylogeny of Feathers

The five stages of the development of feathers reconstructed from ontogeny correspond well with the phylogeny of theropods, indicating a peramorphic trend (fig. 14.4). These evolutionary events in feathers occurred sequentially in nonavian coelurosaurs before the origin of birds. These stages are: (1) a single filament; (2) multiple filaments joined at the calamus base; (3) multiple filaments branching laterally from most of the length of a central filament, or rachis, to form barbs; (4) contour feathers composed of a prominent rachis with barbules; closed symmetric vanes occurring distally on either side of the central rachis and open vanes proximally; and (5) closed asymmetric vanes on either side of the central rachis. These events produced several morphotypes that

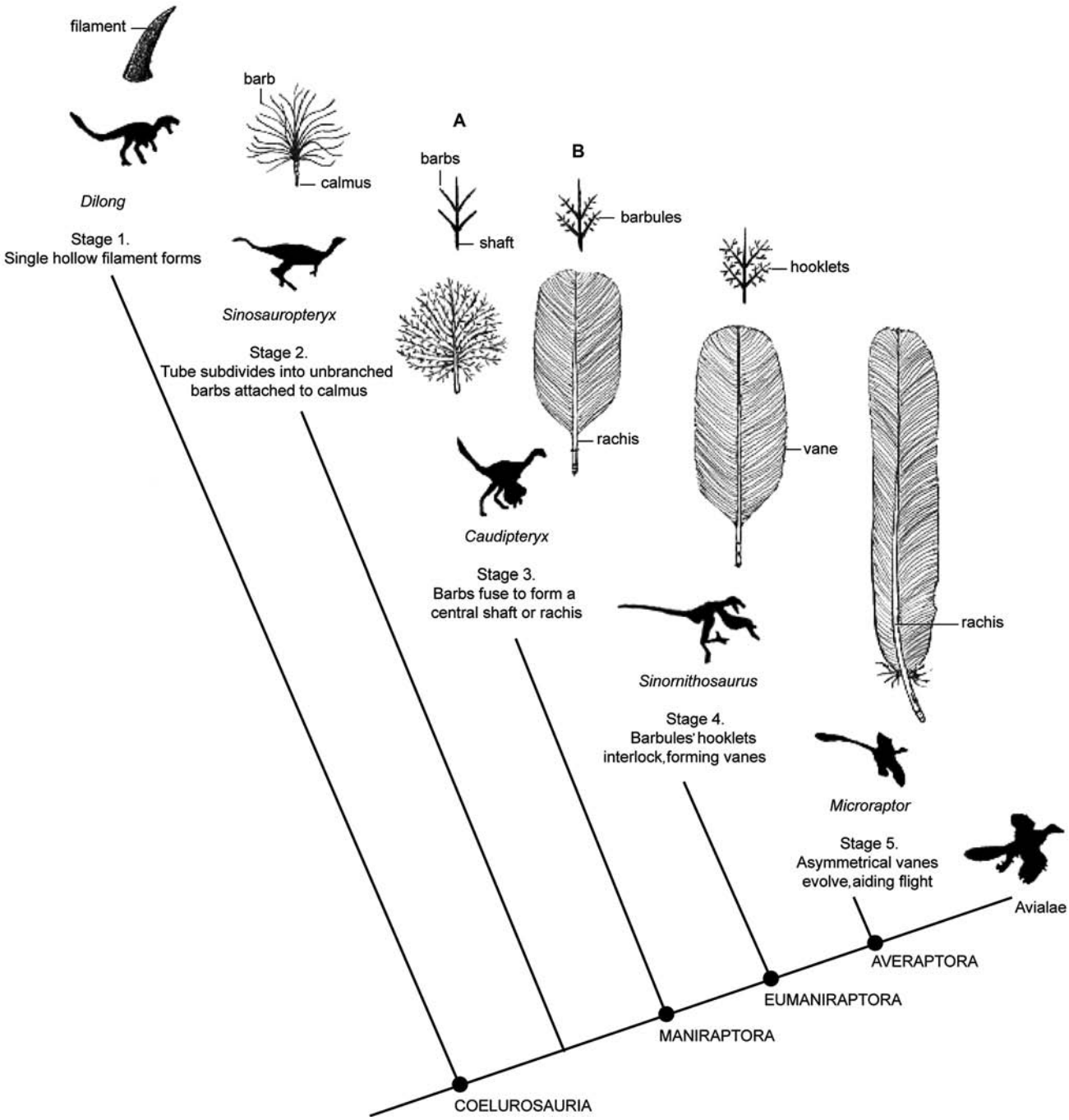


Figure 14.4. Heterochrony of feather evolution showing the peramorphic trend where ontogeny recapitulates phylogeny. Five stages of the developmental model of feather evolution proposed by Prum and Brush (2003), superimposed on the phylogeny of theropods. Stage 1, the first feather is a single hollow filament tube as seen in basal theropods such as *Dilong*. Stage 2, the tube subdivides into unbranched barbs, which are attached to a calamus; this stage is represented by *Sinosauropteryx*. Stage 3A, a feather with barbs and barbules is attached at the base of the calamus (downy feather) as represented in the body of *Caudipteryx*; stage 3B, a planar feather with unbranched barbs is fused to a central rachis (contour feather), represented in the wings of *Caudipteryx*. Stage 4, barbule hooklets interlock, forming closed symmetric vanes to fashion the pennaceous as seen in the wings of *Sinosauropteryx*; stage 5, closed asymmetrical vanes evolve similar to modern flight feathers (the remix and the rectrix) as seen in *Microraptor* and Avialae (modified from Prum and Brush 2003).

coexisted in the coelurosaur lineage for different functions, but the early two stages were probably lost in early avian evolution (Prum and Brush 2003; Xu and Gao 2009; Zimmer 2011).

The most primitive structure of protofeathers (stage 1) may have been a simple, conical, cylindrical filament, as documented in *Dilong*, *Sinosauropteryx*, and *Beipiaosaurus*. Stage 2 feathers with simple downs attached to a calamus and no vanes are encountered in *Sinosauropteryx* and *Beipiaosaurus*. Stage 3 feathers with paired vanes lacking barbules attached to a central shaft appear in *Beipiaosaurus*, *Protarchaeopteryx*, *Caudipteryx*, *Anchiornis*, and *Sinornithosaurus*. Stage 4 feathers, the symmetric vane feathers with the appearance of barbules that link the vanes of a feather into a continuous surface for gliding, are known in *Protarchaeopteryx*, *Sinornithosaurus*, *Caudipteryx*, *Anchiornis*, *Microraptor*, and avialans. Stage 5 feathers, the asymmetric flight feathers, are encountered in the remiges of *Microraptor*, *Archaeopteryx*, *Sinornis*, *Confuciusornis*, pygostlians, and modern birds (Prum and Brush 2003; Xu and Guo 2009).

Recently, McKellar et al. (2011) described a diverse assemblage of isolated fossilized feathers of theropods and early birds from the Late Cretaceous amber deposits of Canada that span the four evolutionary-developmental stages for feathers outlined by Prum and Brush (2003). Using the ontogenetic relationship as a guide, the phylogeny of feathers is reconstructed in a framework of Jehol theropod genealogy (fig. 14.4). It appears there is a nice correspondence between ontogeny and phylogeny of feather evolution in theropod dinosaurs, indicating peramorphism (Chatterjee and Templin 2004a).

The Fossil Record

Fossil feathers are sparse in the paleontological record. Since feathers decay easily, the preservation of these soft, delicate structures requires an unusual setting, such as the calm waters of a lacustrine or lagoonal environment, and rapid burial without any turbulence. Davis and Briggs (1995) discussed the mode of fossilization of feathers. According to them, the feathers of Mesozoic birds were preserved in three forms: imprints, carbonized traces, and amber inclusions (fig. 14.5). From studies with scanning electron microscopes, they concluded that a bacterial glycolax played an important role in the fossilization of feathers preserved as imprints and carbonized traces. Because of its antibiotic properties, however, amber preserves the most perfect fossil feathers. The reported Mesozoic feathers are contours, remiges, rectrices, semiplumes, and downs, often isolated. That down feathers might have been the external covering of the body is shown by the Jurassic bird *Confuciusornis*.

Imprintation

The earliest record of a fossil feather comes from *Archaeopteryx* from the Upper Jurassic of Bavaria (fig. 14.5A). The feathers of *Archaeopteryx* are preserved mainly by imprinting after early lithification of Solnhofen Limestone by bacterial decay. Alan Feduccia (1980) has pointed out that the presence of vane asymmetry in the wing feathers of *Archaeopteryx* indicates their flight capability. There are about twelve primaries and fourteen secondaries arranged in the same basic avian design. Surprisingly, this earliest fossil feather is identical with the structure of the feather of a modern volant bird. Even dark brown pigment is preserved in the isolated feather, as in a thrush. As discussed earlier, a wide variety of imprinted feathers covering the bodies of coelurosaurs and early birds has been discovered from the Jehol biota of China that shed critical light on the origin of feathers and evolution of flight (Xu and Guo 2009).

Carbonized Traces

Carbonized traces are the most common type of preserved feathers found in the Cretaceous sediments (fig. 14.5B–H). The Early Cretaceous records include an isolated contour feather from Montsec, Lerida Province of Spain (Ferrer-Condal 1954), asymmetrical feathers associated with *Concornis* from the Las Hoyas Province of Spain (Sanz and Buscalioni 1992), colored down feathers from Mongolia associated with *Ambiortus* (Kurochkin 1985), three isolated contour feathers from Australia (Waldman 1970), and a semiplume (Martill and Filgueira 1994) and a down feather (Kellner et al. 1994) from Brazil. The solitary

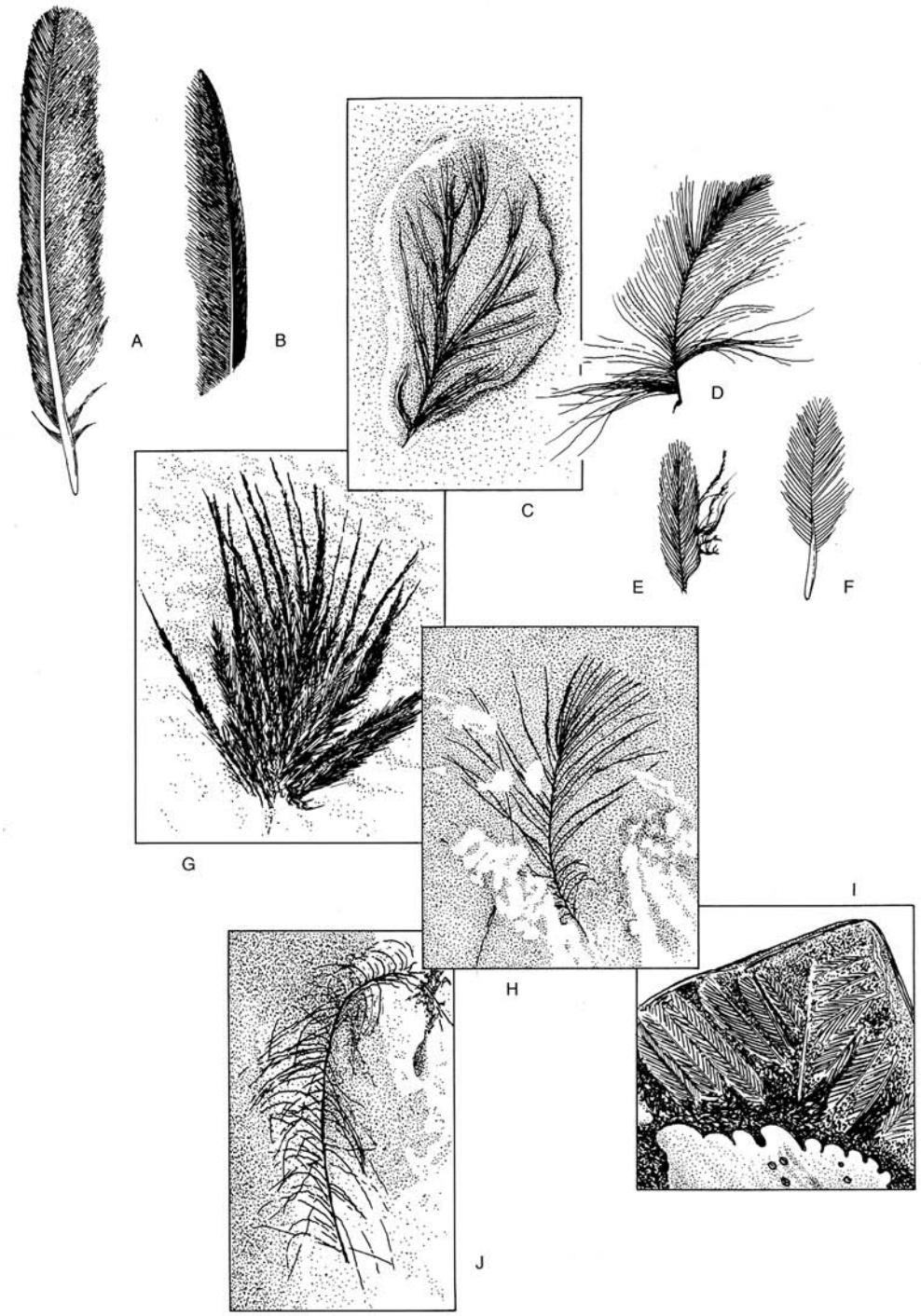


Figure 14.5. Mesozoic fossil feathers were preserved in three ways: imprintation (A), carbonized traces (B–H), and amber inclusions (I–J). A, the solitary remex of *Archaeopteryx* reported by Herman von Meyer in 1861 from the Late Jurassic of Germany; asymmetrical vanes indicate aerodynamic function. B, primary feather that probably belonged to *Ambiortus* from the Early Cretaceous of Mongolia; asymmetrical vanes suggest that *Ambiortus* was a volant bird (Kurochkin 1985). C, isolated down feather associated with *Iberomesornis* from the Early Cretaceous Las Hoyas of Spain (Sanz et al. 1996). D–F, a variety of feathers recovered from the Early Cretaceous sediments of southern Victoria, Australia (Waldman 1970). G, down feather from the Early Cretaceous Santana Formation of Brazil (Kellner et al. 1994). H, semiplume feather from the Early Cretaceous Crato Formation of Brazil (Martill and Filgueira 1994). I, semiplume feather in an amber inclusion from the Early Cretaceous of Lebanon (Schlee 1973). J, semiplume feather in an amber inclusion from the Late Cretaceous of New Jersey (Grimaldi and Case 1995).

record of carbonaceous fossil feathers, the plumaceous type in *Parahesperornis*, comes from the Late Cretaceous deposits of Kansas (Martin 1984). Fossil feathers become more abundant in Tertiary freshwater deposits and are often associated with insect fossils.

Amber

Amber often contains beautiful fossil feathers as inclusions, such as the semiplume specimens from the Lower Cretaceous of Lebanon (Schlee 1973). This is the oldest record of a feather in amber (fig. 14.5I–J). The structure of this feather is reminiscent of certain species of present-day waterfowl. The second oldest amber specimen is known from the Late Cretaceous of New Jersey (Grimaldi and Case 1995). It is also a semiplume feather and probably belonged to a terrestrial bird. Feathers are common in the Late Cretaceous amber deposits of Alberta, Canada (Martill and Filgueira 1994). Recently a diverse assemblage of feathers has been discovered from the Late Cretaceous amber deposits from Grassy Lake, Alberta, Canada. Specimens include an array of feather structure and pigmentation including filaments similar to protofeathers of *Sinosauropteryx* to highly derived asymmetric contour feathers for flight as seen in birds (McKellar et al. 2011).

Feather Colors

Birds are among the most brilliantly colored members of vertebrates with iridescent sheens and brilliant streaks and splashes. Besides songs, birds also communicate visually. The intricacies of feather microstructure and pigments combine to produce stunning effects in plumage. Feather colors come in all shades, hues, and tints, due either to biochrome pigments deposited in feather microstructure or to special features of feather surfaces. Bird feathers show color in two ways, pigmentation and structure. Pigments produce most colors in nature. There are three major kinds of pigments found in bird feathers: melanins, the most common pigments, produce grays, blacks, and browns; carotenoids, intense red and bright yellow colors; and porphyrins, a range of reds, browns, and some green hues. Birds derive some pigments such as carotenoids from external sources such as plants and animals. For example, flamingos and scarlet ibis get their spectacular red color from small crustaceans during feeding. If these birds are deprived of their natural food in zoos, they lose their red color.

Other colors are created not by chemical pigments but by physical structures within the feathers. In many birds, the colors in feathers are formed from light refraction caused by the structure of the feather. The best-known example is the throat feathers of many hummingbird species. Structural colors are of two kinds, iridescent and noniridescent. Iridescent colors are shimmering colors that change according to the angle at which light hits the feather surface, and they have a metallic effect. This color comes from a particular modification in the shape of the filament of the feather. Noniridescent colors such as the bright blue feathers found in many birds are produced by nanostructures, microscopic bubbles in the keratin of feathers, which refract and scatter the light. These colors do not change according to the angle at which light hits the feather's surface. These two sources of color, chemical and physical, are sometimes combined in the same feather.

As one might expect from the amazing diversity of colors and patterns exhibited by birds, birds can see tetrachromatic colors: red, blue, green, and ultraviolet light and their combined hues (Hill and McGraw 2006). Color vision among vertebrates is a result of having specialized light receptor structures known as rods and cones at the back of the eye in the retina (Allman 1999). Rods are extremely sensitive to even dim light but provide relatively coarse, colorless images. Birds have perhaps the most advanced visual system of any vertebrate with well-developed cones (Goldsmith 2006).

The origin of color vision in birds remains enigmatic but the Daohugou-Jehol coelurosaurs offer interesting clues about feather colors and function: that feathers first evolved to be seen (Zimmer 2011). Identification of color-imparting microscopic sacs inside the feathers of Liaoning coelurosaurs, called melanosomes, that correspond precisely in shape to structures associated with specific colors in the feathers of living birds indicate that these

feathered theropods had developed vibrant color plumages. The scientists found two kind of melanosomes buried within the structure of fossil feathers, which are tough proteins and can be preserved: sausage-shaped organelles called eumelanosomes that are seen today in the black masks of cardinals; and spherical organelles called phaeomelanosomes, which make the pigment that creates the rusty reds of red-tailed hawks. Using these melanosomes, scientists have decoded the true color of feathered coelurosaurs. For example, *Sinosauropteryx* exhibited chestnut to reddish-brown tones of protofeathers running in alternate orange and white rings down the tail (Zhang et al. 2010). The feathers of the biplane *Microraptor* had a glossy iridescent sheen in hues of black and blue, like a crow (Li et al. 2012). The function of iridescent colors in feathered coelurosaurs and early birds has centered on their roles as visual social signals. Similarly, for the Late Jurassic *Anchiornis*, the body was gray and dark, the wings were black and white striped, and the face had rusty red crown (Li et al. 2010). Some reconstructed Liaoning feathers appear to have developed a plethora of extravagant colors; they retain vivid, banded color patterns and elongate, ribbon-like tails in many forms, indicating that color vision had already developed in Chinese coelurosaurs. Recent phylogeny of melanosome evolution suggests that there is an abrupt increase of melanosome diversity in maniraptorans in concert with the development of contour feathers leading to birds (Li et al. 2014).

Sexual selection is directed by female choice or mate-mate competition and results in traits that lead to mating success (Darwin 1871). Usually a female bird chooses a mate from among the available males on the basis of certain conspicuous physical traits, such as coloration, increased size, or striking adornments that make a bird more attractive. The plumage color can encode information about the fitness of a potential mate. Mate choice is a critical driving force in the evolution of a species because it is central to an animal's strategy for perpetuating itself. Feather coloration possibly allowed evolution of elaborate rituals of theropods; these were advantageous in mating. The extraordinary development of color vision in birds might have originated from the arboreal proto-birds, conferring several advantages: camouflage, foraging for ripe fruit or colored insects, providing food for chicks, and finding a suitable mate (Chatterjee and Templin 2012). Later, as feathers became elongate and complex with fully developed airfoils, they were co-opted for flight.

Footprints

Bird tracks are very distinctive because of their tridactyl or tetradactyl configuration. Footprints reveal much about the anatomy, ecology, speed of locomotion, habits, and behavior of birds. The size and shape of the footprints, the number of toes, their spreading angle, and their arrangement serve to identify birds and to provide us with clues to their mode of life. Prints that show partially webbed feet indicate an aquatic existence. Perching birds generally hop on the ground and leave their prints paired. Gamebirds, on the other hand, generally walk or run; thus, their track pattern consists of a series of alternate prints.

Mesozoic bird tracks are relatively poorly known compared to the tracks of nondinosaurs. In recent years there has been an increasing number of reports of footprints of Mesozoic birds from East Asia, Africa, and North America. These tracks extend the geographic distribution of birds and suggest their diversity. Martin Lockley and associates (1992) reviewed the classification and distribution of the ichnofauna of Mesozoic birds. These avian tracks are small, about 2 to 6 centimeters long, and are identical to those of modern birds. They are generally tridactyl or tetradactyl with slender digit impressions. There is a wide divarication angle between digits 2 and 4, the hallux is caudally directed, and the claws are slim (fig. 14.6).

The earliest record of bird tracks comes from the Late Triassic Manassas Sandstone in the Culpepper Basin of Virginia, which is coeval with the Dockum Group. Robert Weems and Peter Kimmel (1993) described these small tridactyl bird tracks as *Plesiornis pilulatus* (fig. 14.6A). The prints are small, about 3 centimeters long, with narrow toes and indistinct footpads; the divarication angle between digits 2 and 4 is 70°. Weems and Kimmel

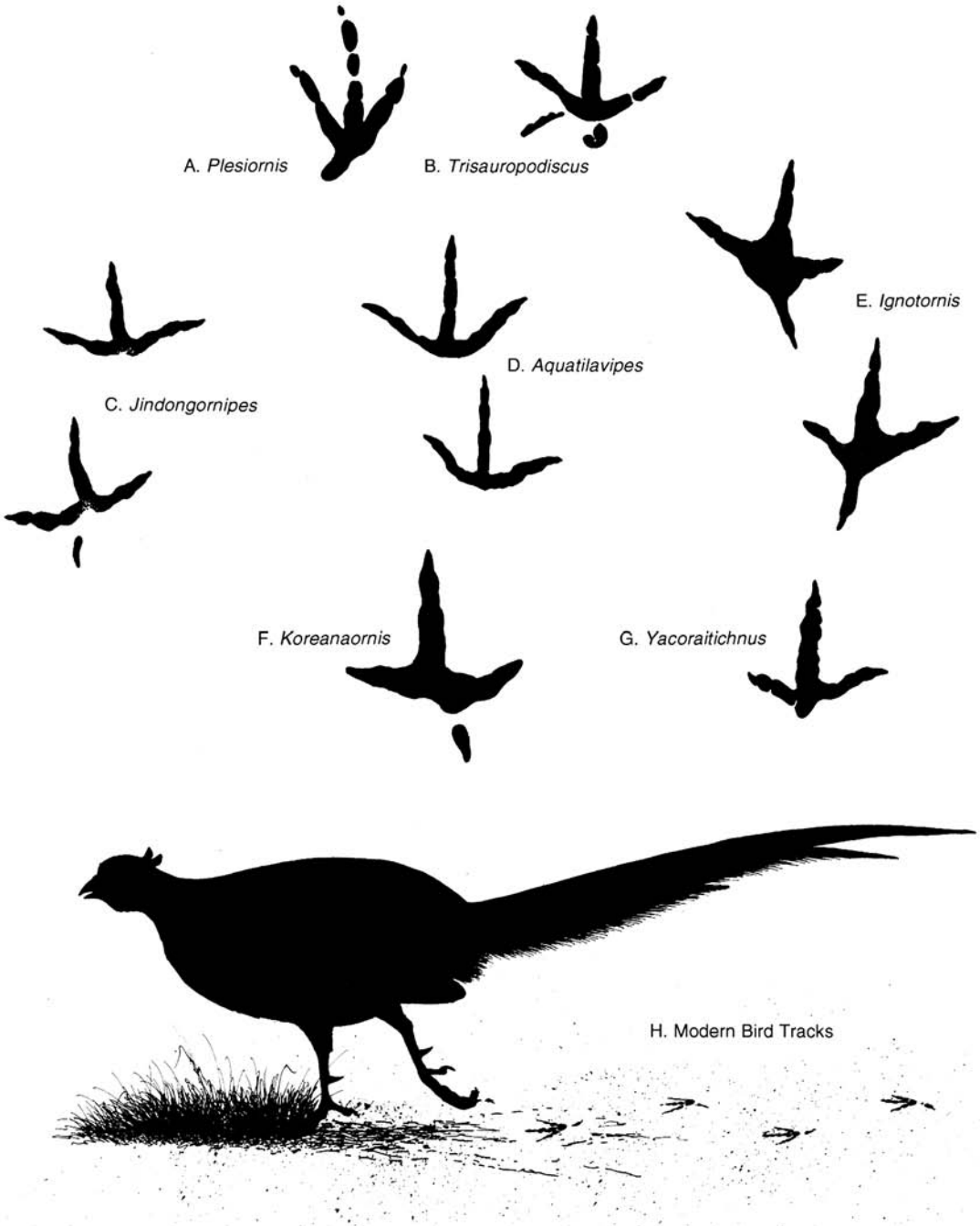


Figure 14.6. Bird tracks. A, *Plesiornis* track from the Late Triassic Manassas Formation of Virginia. This earliest bird track was probably made by a *Protoavis*-like animal; similar tracks are also known from the Late Triassic of Argentina and the Early Jurassic Portland Formation of Massachusetts (Weems and Kimmel 1993; Lull 1953). B, *Trisauropodiscus* tracks are known from Early Jurassic rocks of Africa, Morocco, and North America (Ellenberger 1972). C, *Jindongornipes* tracks from the Early Cretaceous of South Korea (Lockley et al. 1992). D, *Aquatilavipes* tracks from the Early Cretaceous of Canada (Currie 1981). E, Ignotornis tracks from the Early Cretaceous of Colorado (Lockley et al. 1992). F, *Koreanaornis* track from the Early Cretaceous of South Korea (Lockley et al. 1992). G, *Yacoraitichnus* track from the Late Cretaceous of Argentina (Alonso and Marquillas 1986). H, bird tracks produced by a ring-necked pheasant (*Phasianus colchicus*).

concluded that these tracks were made by a *Protoavis*-like bird. *Plesiornis* was originally described from the Early Jurassic Portland Formation of Massachusetts (Lull 1953).

The next oldest record of bird tracks is reported from the Early Jurassic rocks of Africa and North America. Ellenberger (1972) described several varieties of *Trisauropodiscus* (fig. 14.6B) from the Stormberg Beds of South Africa. These slender tridactyl or tetradactyl toes range in size from 2 to 7 centimeters, with a large divarication angle. Similar tracks are known from the contemporary beds of North America and Morocco. The Upper Jurassic bird tracks are poorly known except for the dubious footprints from Ribadesella, Spain. The existence of these Late Triassic and Early Jurassic bird trackways is exciting. It suggests that birds were numerous and widespread 50 to 75 million years before the appearance of *Archaeopteryx*, thus filling important gaps at a crucial time in the history of bird evolution.

Bird tracks are abundant and dense in the Early Cretaceous deposits. Many of these footprints were made by shorebirds and waders. Interesting ichnotaxa include *Jindongornipes* (fig. 14.7C) from the Jindong Formation and *Koreanaornis* (fig. 14.6F) from the Haman Formation of South Korea, *Ignotornis* (fig. 14.6E) from the Dakota Group of Colorado, and *Aquatilavipes* (fig. 14.6D) from the Gething Formation of Canada (Lockley et al. 1992). These tracks are generally tetradactyl with a caudally directed hallux, and the second and fourth digits show a high divarication angle. The footprints average 4 to 5 centimeters wide and 3 to 6 centimeters long. Bird tracks similar to those of *Aquatilavipes* are also known from Japan and China. The abundant track records of Early Cretaceous birds indicate their adaptive radiation and diversity in lacustrine and shoreline environments.

Late Cretaceous bird tracks are poorly documented. The earliest recorded webbed foot tracks are from the Uhangri Formation of South Korea and were probably made by a flamingo-like bird. These tracks were not named or described in detail. Probable bird tracks are also known from Utah and Morocco, but detailed description is not available. Alonso and Marquillas (1986) reported bird tracks from the Late Cretaceous of Argentina that display clear digital pad impressions (fig. 14.6G). Some bird tracks from the Dunvegan Formation of Alberta may be attributable to hesperornithiform birds (Lockley et al. 1992).

Terrestrial Locomotion

Fossil footprints reflect the bipedal terrestrial locomotion of birds. They are not merely an impression of the undersurface of the bird's feet, but are a product of the kinetic interaction of footfall with the substrate, reflecting the symmetrical feet and digitigrade stance of birds, where the metatarsals are fused into the tarsometatarsus and the heels are permanently lifted from the ground. Birds essentially spend their lives standing on tiptoe. Most birds have toes arranged in an anisodactyl manner, with three toes pointing forward and one toe pointing to the rear. This is why tridactyl footprints are common. From footprints, the mode of locomotion of birds can be inferred. Like us, birds walk to go slow and run to go faster. During walking, they move their feet alternately, setting one down before the other is lifted. In running, the feet move alternately, but during hopping, the feet move together and are set down side by side.

Among flying vertebrates, birds are greatly superior to bats and pterosaurs in supporting the wings entirely by the forelimbs, so that the hindlimbs are free and the animal can walk and run. Birds are obligate bipeds, and their forelimbs play no role in supporting weight during terrestrial locomotion. They have dual locomotor systems: the wings and tail for flying and the legs for walking, running, hopping, or swimming. Birds inherited the bipedal posture and locomotion from their theropod ancestors. Since both groups share erect, bipedal digitigrade locomotion, there has been a tendency in recent times to reconstruct the locomotor pattern of nonavian theropods in the fashion of modern birds, assuming both groups were dynamically similar and walked and ran in very similar ways (Paul 1988). However, comparative functional analysis suggests that there are some major differences in the kinematics of hindlimbs between these two groups. Many of the differences of the locomotory refinement in birds may be attributed to the size of the tail and its musculature

and subsequent changes in the position of the body's center of gravity, femoral orientation, the femoral-tibial ratio, and transfer of the main hindlimb motion from the hip to the knee joint.

Steve Gatesy of Brown University has provided valuable insights into the functional evolution of the hindlimb and tail from basal theropods to pygostilian birds (Gatesy 1990, 1995). The functional differences in bipedal locomotion between these animals are principally related to the size of the tail and its musculature. In nonavian theropods and avialans, hindlimb locomotion is principally powered by the tail (caudofemoral) muscle that pulls the vertically held femur backward; they retract the hindlimb by extending the hip joint. In pygostilian birds, with the loss of the bony tail, the caudofemoral muscle became substantially reduced and is not used for femoral retraction. The tail is decoupled from terrestrial locomotion and serves an entirely different function (controlling the position of tail feathers). In these birds, the femur is relatively short, buried in muscle, and held more horizontally. To stand easily and walk on land, however, feet need to be placed near a bird's center of gravity. With the loss of the tail, as the center of gravity shifted forward in pygostilian birds, the horizontal femurs pushed the feet relatively forward to align with the center of gravity. Because the lower parts of the legs have little musculature, they have to be controlled by a pulley system from the muscles at the top of the leg where protractor and retractor muscles are located anterior and posterior to the hip. The swinging of the tibiotarsus at the knee joint carries out the locomotion. The motion of the distal limb segments transforms the alternating forward motion of the feet into a continuous forward motion at the knees and thus assures propulsion. Nonavian theropods moved their columnar limbs more like humans, with a large arc of rotation at the hip joint, whereas birds move with their femora oriented subhorizontally and their knees highly flexed. The main functional movement in birds has been shifted from the hip to the knee joint (fig. 14.7). These topographic differences in the main functional joint reflect further refinement in avian locomotion from the ancestral theropod condition.

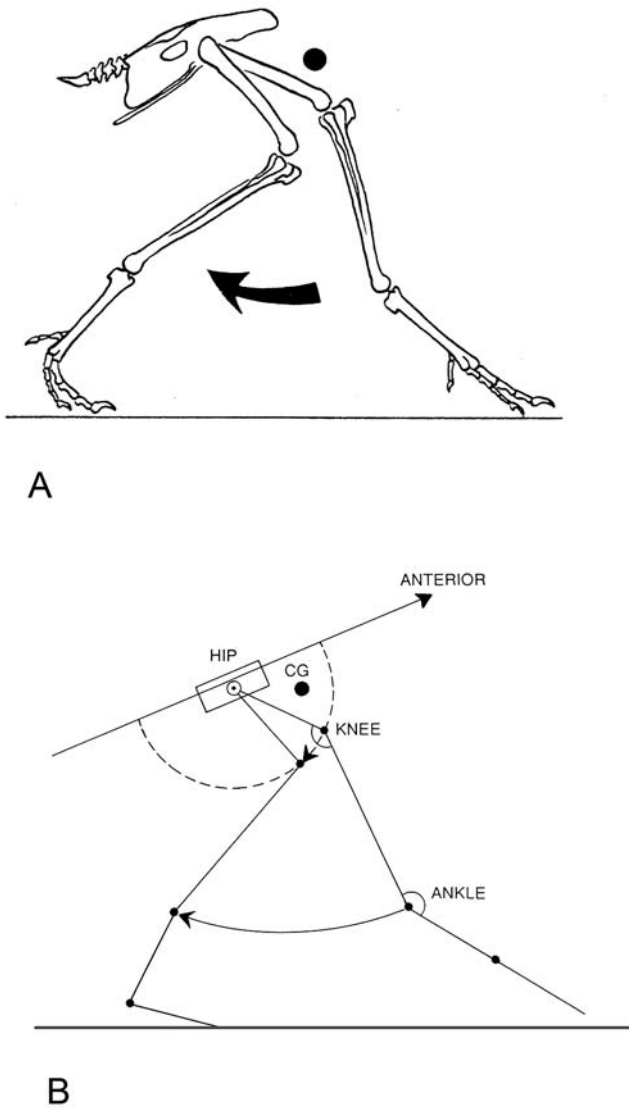


Figure 14.7. Functional evolution of the hindlimb and tail of pygostilian birds from theropod condition. In nonavian theropods, the tail muscles retract the vertically held femur backward during locomotion; the main movement is in the hip joint A, in pygostylians such as the modern bird *Numida*, with the loss of the bony tail, movements of the knee, rather than femoral retraction, account for most of the foot displacement (after Gatesy 1990). B, stick diagram showing the bipedal locomotion of pygostylians; note that the subhorizontal femur undergoes a relatively small excursion. Most of the foot flexion is produced by knee flexion (arrow); the solid circle represents the center of gravity (after Chatterjee 1999).

The longer the leg, the longer the stride. Running dinosaurs and birds increase the effective length of their legs by standing on their toes, keeping their heels high off the ground. Traditionally the relative lengths of the upper and lower segments of the hindlimbs have been used as measures of running potential (Gregory 1912). In a cursorial animal, the lower segment (tibiotarsus) is considerably longer and slimmer than the upper segment (femur). The femoral-tibial index ranges from 130 to 82 in nonavian theropods. Birds show much more disparity of hindlimb proportions than do other theropods. Of the birds sampled, the femoral-tibial value ranges from 78 to 58; the lowest index in ostriches indicates their superb cursorial ability. With the loss of flight, terrestrial locomotion is highly refined in ratites with the development of long and powerful legs and by reduction of the size of the foot.

15 The Feeding Mechanism and Cranial Kinesis

His beak is focused; he is preoccupied,
looking for something, something.
Poor bird, he is obsessed.

Elizabeth Bishop, *Sandpiper*, 1965

Flight demands so much energy that birds must feed frequently to refuel. They have insatiable appetites and plunder a wide variety of food that suits their needs with the highest energy profit. In birds, the forelimbs evolved into wings for flight that can no longer grasp and rip food. Instead, birds use their bills to secure and process food. The long, flexible neck with heterocoelous vertebrae permits a wide range of movement to the head during feeding. Neck flexibility and upper jaw mobility transform the avian bill into a universal tool. Adaptations for feeding are an important module of avian evolution. With elimination of teeth, jaws can change shape in response to feeding behavior. Although the avian body plan is fairly uniform for flight requirements, beak diversity is high because the rhamphotheca, the horny covering of the bill, can be relatively easily modified. Most birds—with the exception of parrots and birds of prey—catch and hold their food with their bills alone. Development of the bill as an independent, enlarged, and variable segment of the skull is characteristic of birds, and its shape and structure are highly correlated with foraging methods and food. It is extraordinary how versatile and effective a bill can be for procuring food.

One reason birds are so successful is that they can eat almost anything—plants, insects, small animals, and food that is inaccessible to others. The main functions of the bill are to expose, seize, kill, and prepare food for swallowing. When a bird acquires a food item, it must manipulate it for swallowing by removing inedible parts. The birds' lack of teeth limits the elaborate chewing and maceration of food into more edible pieces before swallowing. Birds simply swallow food whole; the digestive system is designed to process unmasticated food, including both storage and digestion. The food is not processed orally but passed through the esophagus, which is expanded in some birds into a holding tank, or crop, to store and soften food. The food then passes to the two-chambered stomach, the anterior proventriculus and the posterior gizzard. The proventriculus is most developed in fish-eating birds and raptors. The avian gizzard—the functional analogue of mammalian molars—is a large, strong muscular structure that contracts rhythmically to grind and break down food. To increase the efficiency of the grinding action of the gizzard, many birds fill it with abrasives by swallowing grit

or stone. In carnivorous birds, the gizzard acts as a trap for sharp bones and other indigestible fragments. These items are rolled into a ball and regurgitated as a pellet. For example, hawk and owl pellets provide important clues about indigestible food items, such as bones, fur, feathers, claws, and teeth.

The bill has evolved into a wide range of sizes and shapes in response to a vast spectrum of food: plants, seeds, fruits, insects, invertebrates, fish, meat, mixed diets, and even microscopic planktons. Birds exploit every category of plant and animal life on Earth in every environment—forests, mountains, grasslands, scrub, marshes, deserts, tundras, rivers, lakes, islands, and oceans; they have even encroached on farms, cities, and landfills in search of food. Food, water, protective cover, and a sheltered place to nest and breed are basic to a bird's survival. There is often enough food for birds in the wild, but they are opportunists. They will take advantage of whatever sources they can find. Generally, most birds feed on a variety of foods that can change substantially, depending on the season. Many birds migrate seasonally hundreds of kilometers in search for their food in changing environments where the food and water supply can dwindle or disappear, plant cover can vanish, and competition with other animals can increase.

Multitasking Bills

A bird's bill is used for multitasking functions such as feeding, preening, manipulating objects, killing prey, defending against intruders, fighting, probing for food, courting a mate, singing melodies, and feeding young. Birds may bite or stab with their bills to defend themselves. Some species use their colorful bills for courtship display. Brightly colored bird bills indicate good health and attractiveness to the opposite sex. Like feathers, the color of a bird's beak results from concentrations of pigments such as melanin and carotenoid.

The bill is the key adaptation for feeding in birds, and it is shaped according to what a bird eats. The bill is the most versatile part of the feeding system. The primary functions of the bill are to expose, seize, kill, and prepare food items for swallowing. There are many bill adaptations, depending on food source, with some bills adapted to general foraging and others highly specialized. Different bill types have evolved for catching insects, stabbing and seizing prey, tearing flesh, capturing and holding fish, cutting and crushing seeds, probing tree crevices and mud, chiseling wood, filtering planktons, and so on. The morphology of the bill gives clues about the food preference of a bird.

The seed-crackers have short, cone-shaped beaks so that they can crack open their food with as much force as possible. Finches have short, heavy, and sharp bills operated by strong jaw muscles for breaking open seeds and nuts. Thin, slender, pointed tweezers-like beaks are found mainly in insect-eaters such as warblers. The waders have long, pointed beaks to pluck earthworms and insect larvae from damp ground. Pelicans, gannets, boobies, terns, and kingfishers locate their fish prey from a perch and capture their prey by plunge-diving from the air into the water by thrusting their long, heavy, wedge-shaped bills. Birds that feed on slippery prey, such as fish, have bills whose keratinized margins are serrated to improve friction grip. The flamingo uses its highly recurved beak, which is fringed at the edges, under the water "upside down" for sieving of diatoms and algae. The parakeet's strong curved bill is well adapted for cracking seeds, and its hooked tip is used to pull at the pulp of fruit. Many fish-eaters have long, hooked beaks for catching fish and ripping them apart. Birds like loons, herons, and kingfishers have spear-like bills for impaling fish. Woodpeckers use their strong beaks, which taper to the tip, to pick large insects out of crevices in trees. Hummingbirds have long, tubular bills that resemble straws, which they use to sip nectar from flowers through capillary-like tongue tips. Geese are among the few birds that have developed broad bills for tearing grasses. Many ducks strain plant and animal food from water. The edges of mallard's bill are fringed to strain plants, seeds, and small animals from mud and water. The bill is swung back and forth sideways, while the mandible pumps very fast to strain food particles. Fish-eating ducks such as mergansers have serrated edges to their bills to help them grip their prey. The oystercatcher feeds on seashore invertebrates and has

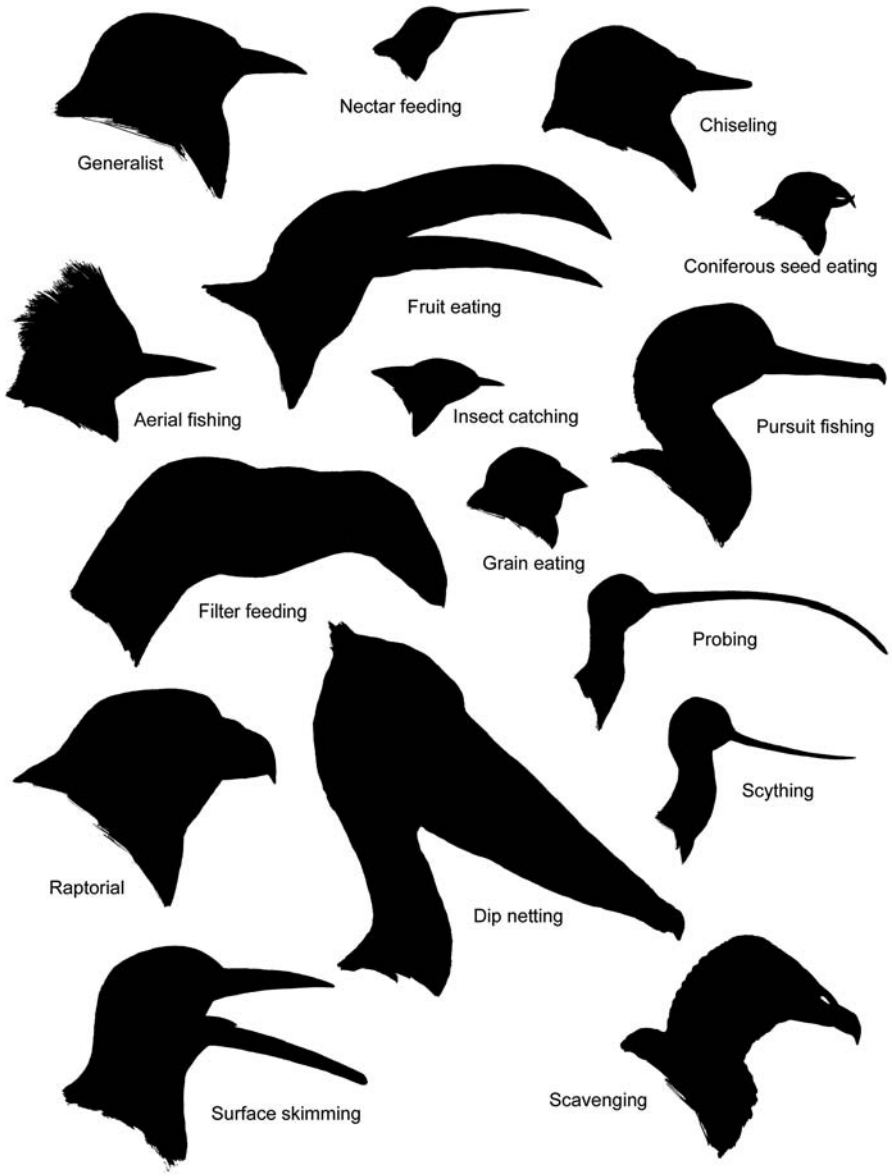


Figure 15.1. Examples of bills adapted to different kinds of feeding.

developed a hammer-like bill tip to smash through the shells. The birds of prey such as hawks, owls, and eagles have strong, hooked beaks with which they tear flesh and sinew. These formidable beaks are used to bite the skull or neck and also to tear the body into pieces small enough to swallow. The carrion-eating vulture and caracara have sharp hooks at the tips of their beaks for tearing hides and meat. The shoebill's beak ends in a hook, but it is flat and serrated as an aid in holding slippery frogs. The crows have a multipurpose bill that allows them to eat fruit, seeds, insects, fish, and other animals (fig. 15.1).

Bird bills are iconic for evolutionary and ecologic studies. The variation in sizes and shapes of bills in thirteen species of Darwin finches from the isolated islands of the Galapagos archipelago, each filling a different niche on different islands, is a prime example of adaptive radiation and evolution. Recent work by Peter and Rosemary Grant of Princeton University has documented how the beak

size of Darwin finches repeatedly changed within three decades as a response to environmental changes during El Niño conditions and the availability of their diets of seeds (Grant and Grant 1992, 2008). Those individuals that survived during the severe droughts passed their characteristics on to the next generation, illustrating natural selection in action. Smaller finches with less-powerful beaks perished in the harsh conditions. The variation of beaks also illustrates how a variety of different species of birds can evolve from a single lineage in recent times, a fast forward example of Darwinian evolution.

Four major features make up the general morphology of bird bills: the upper jaw, the lower jaw, the nasofrontal hinge, and an outer horny sheath. The bill consists of a bony interior of upper and lower jaws, which are covered with a thin horny sheath of keratin, called the rhamphotheca. The rhamphotheca is constantly growing—like human fingernails—but it is subjected to constant wear, which maintains its proper length (fig. 15.2A). In a dried skull, the rhamphotheca is generally lost, leaving the bony framework.

In birds, bills develop early in embryonic life in the first week of development, when mesenchyme derived from the neural crest gives rise to skeletal projections of upper and lower jaws (fig. 15.2B). Two signaling molecules, fibroblast growth factor 8 (Fgf8) and sonic hedgehog (Shh), control the process of bill formation at this early stage and induce cartilage outgrowth. The domain expression of the Fgf8 is the dorsal fronto-nasal primordium (FNP) and the ventral nasal primordium (MNP). The intervening region is the domain Shh (Grant and Grant 2008).

Although bills may seem rigid, they possess some flexibility. The bony upper jaw attaches to the braincase by a thin, flexible sheet of bone called the nasofrontal hinge so birds can flex or bend the upper half of the bill at this hinge, an ability called cranial kinesis. The fusion of the rest of the skull bones around the braincase has provided a rigid, stationary unit for the bill. Selection pressure has transformed the upper jaw into a mobile unit, which is hinged to the stationary braincase to form a kinetic skull. Manipulation of objects by the bill involves the motion

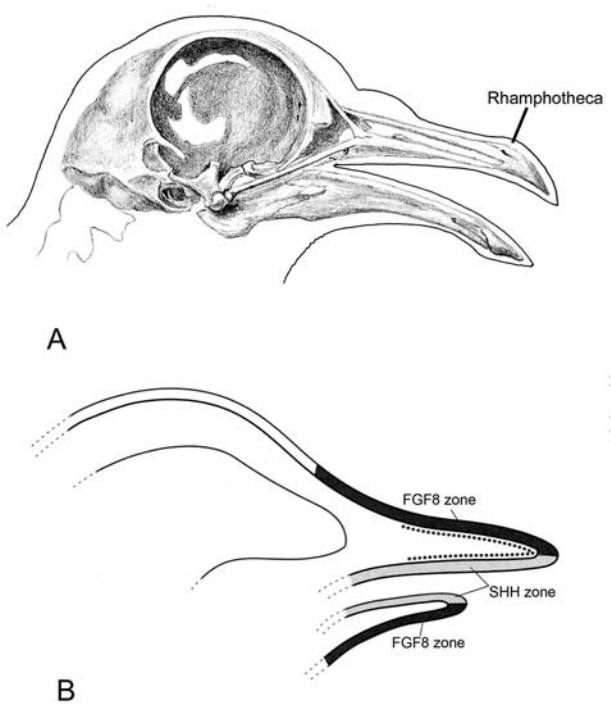


Figure 15.2. Parts of a bill. A, a bird's bill consists of a horny sheath, called the rhamphotheca, supported by an internal bony framework made up of the upper and lower jaws. B, a bill in the early stages of development. Two signaling molecules, fibroblast growth factor 8 (Fgf8) and hedgehog (Shh), induce cartilage outgrowth of the upper and lower mandibles (simplified from Grant and Grant 2008).

of both jaws. To understand the function and evolution of feeding mechanisms in birds, we must have a thorough understanding of the anatomy and functional morphology of their feeding apparatus. Cranial kinesis is the motion of the upper bill relative to the braincase, which always includes pivoting of the quadrate on the braincase and sliding of a palatal unit. Cranial kinesis, or lack thereof, is usually linked to feeding. Animals that must exert powerful bite forces, such as mammals or crocodiles, lack kinesis for maximum strength. Most vertebrates, such as crossopterygian fish, several amphibians, some lizards, and all snakes and birds have kinetic skulls for manipulating food.

Most Mesozoic birds possessed teeth with different morphologies associated with diverse food preferences. Along with the acquisition of cranial kinesis, modern birds became toothless with the development of a horny

beak and a muscular gizzard that functionally replaced dentition for food acquisition and processing. A flexible horny beak allowed a wide range of lateral and palatal bending zones along the length of the beak to facilitate a wide repertoire of cranial kinesis. Once the jaws were freed from teeth, diversification of beak shapes took place in modern birds soon after the KT extinction.

Cranial Kinesis

Avian cranial kinesis is central to understanding the form and function of the entire avian head. The avian feeding apparatus comprises a complicated network of jaw muscles and an intricate system of intracranial mobility. Cranial kinesis (mobility of the upper beak) with a movable or streptostylic quadrate is a fundamental property of all birds. All modern birds have kinetic skulls in which the upper bill can move relative to braincase. Bending between the upper jaw and the braincase occurs in front of the orbit either between the frontal and nasal bones (prokinesis) or within the nasal bone (rhynchokinesis). Much of the diversity of avian heads reflects features related to cranial kinesis with a streptostylic quadrate (Zusi 1993). Birds are well known for their prokinetic skulls and extremely wide gape, which are integral parts of their feeding behavior. Bock (1964, 1999, 2002) and Bühler (1981) summarized the basic pattern of avian kinesis with a two-dimensional biomechanical model and Zusi (1993) reviewed the functional diversity among extant birds.

Although avian cranial kinesis has been known for more than 250 years, its biological significance is not fully understood. It confers several advantages (Bock 1964; Bühler 1981; Zusi 1984, 1993). There are seven potential biological roles of cranial kinesis in birds:

1. passive maintenance of the mandible in a closed position
2. increased size of the mouth opening to facilitate rapid feeding
3. maintenance of the primary visual axis of orientation while the upper bill is raised
4. faster bill closing because both jaws close simultaneously
5. shock-absorbing mechanism for all forces acting on the jaws, permitting a lighter construction of the skull that may function not only in feeding but also in preening, pecking, singing, and nest building
6. increased area for attachment of jaw muscles that may even facilitate singing in some birds
7. skilled manipulation of food by sliding one part of the bill lengthwise in relation to the other and by creating a wedge between the parts that opens backward into the mouth, thus preventing food from escaping

The fundamental advantage of the kinetic apparatus in birds is the potential versatility of the jaws as a manipulatory tool (Zusi 1967; Beecher 1962).

The evolution of cranial kinesis in birds is considered one of the major adaptive breakthroughs in feeding behavior that contributed to the biological success of this group. Hoese and Westneat (1996) speculated that cranial kinesis in birds might be linked to song production. Bout and Zweers (2001) suggested that cranial kinesis is a consequence of general design rather than an adaptive trait. They argued that it has evolved as a consequence of an increase in the size of the orbit that led to the reduction of the anterior part of the skull in the form of a movable bony bars and joints.

Biomechanics of Cranial Kinesis

All modern birds are able to move the upper jaw, or part of it, with respect to the braincase. The upward and downward motions of the upper jaw are usually referred to elevation (protraction) and depression (retraction), respectively (fig. 15.3). Cranial kinesis, or movement of the upper jaw, depends on kinetic bones behind the upper jaw that form an integrated linkage mechanism. The braincase is stationary during jaw movement and connects to the upper jaw by a flexible lamina of bone, which acts as a hinge joint. The flexible joint in the upper jaw is called the nasal-frontal (N-F) hinge. The quadrate head articulates dorsally with the braincase via a double ball-and-socket joint and swings forward and backward like a pendulum. The most widely accepted model for upper

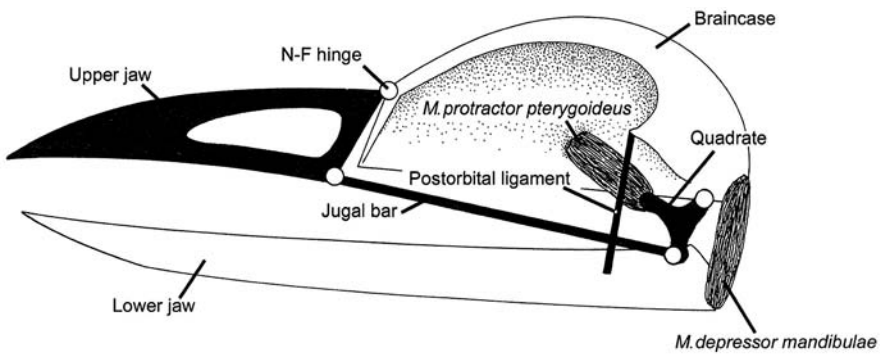


Figure 15.3. Cranial kinesis of a bird based on close chain mechanisms. The skull has several kinematic units—the upper jaw, jugal bar, palatal bar, quadrate, lower jaw, and postorbital ligament—and one stationary unit—the braincase. As the jaw is depressed, the quadrate is swung forward and the upper jaw is raised.

jaw elevation is that the quadrate rotates rostrally and medially toward the pterygoid by muscles, transferring force to the mobile pterygoid-palatine complex, which in turn pushes against the base of the upper jaw, rotating it about the nasal-frontal joint and raising the upper jaw. In this way, the forward and backward movement of the quadrate controls avian kinesis (fig. 15.3). Manipulation of objects involves motion of both jaws, which are linked to the pivotal quadrate. They may be further coupled by the postorbital ligament or by the mandibular articulation (Bock 1964).

Cranial kinesis includes four functional units and four principal joints on each side of the skull (Bock 1964; Bühler 1981; Zusi 1984; Alexander 1983; Chatterjee 1991, 1997): (1) upper jaw, (2) jugal bar + pterygoid-palatine bar, (3) quadrate, and (4) braincase. These four units form a four-bar crank chain mechanism of mobility 1. It has four links and four joints (fig. 15.4A, 15.4B). Because the jugal bar and the pterygoid-palatine bar share similar mechanical functions as a pushrod between the movable quadrate and the upper jaw, they are considered functionally as a single unit to simplify the model. Moreover, the thin jugal bar usually bows outward during jaw opening, but does not contribute significantly to the mechanism producing upper jaw elevation. Thus, the upper jaw, the pterygoid-palatine bar (or jugal bar), the quadrate, and the braincase form a four-bar crank chain in each side.

In modern birds, three main types of kinesis are recognized relative to the position of the dorsal flexion zone and the nature of the nasal opening (Bock 1964; Bühler 1981; Zusi 1984): prokinesis, rhynchokinesis, and amphikinesis (fig. 15.5). Prokinesis and rhynchokinesis are dominant among living birds, whereas amphikinesis is found only in rails. In prokinesis, bending occurs at a single transverse axis across the nasal-frontal (N-F) hinge, so that the entire upper jaw moves as a rigid unit. Prokinesis is associated with a holorhinal naris, where the caudal margin of the narial opening is firm and fairly rounded, making deformation within the upper jaw impossible (fig. 15.6A). In amphikinesis, there are two zones of flexibility within the dorsal bar. The narial opening extends back almost to the nasal-frontal hinge. During protraction, the entire upper jaw is raised and the tip of the jaw is bent up as well.

In rhynchokinesis, the dorsal flexion zone of the upper jaw has been displaced forward from the craniofacial hinge, so that its rostral part can be moved (fig. 15.6B). In this framework, the upper jaw consists of a median dorsal bar, a pair of ventral bars, a pair of lateral bars, and the bony tip (fig. 15.14B). The location, number, and extent of the hinges on the dorsal bar characterize different forms of rhynchokinesis. Zusi (1984) recognized five categories of rhynchokinesis: distal, central, extensive, double, and proximal. Rhynchokinesis is generally associated with the schizorhinal naris where the lateral bar is flexible and the narial opening forms a slit that extends backward beyond the N-F joint. Rhynchokinesis is a unique adaptation. It allows many birds to use their beak tips like a probe to reach buried grabs or insects embedded in tree

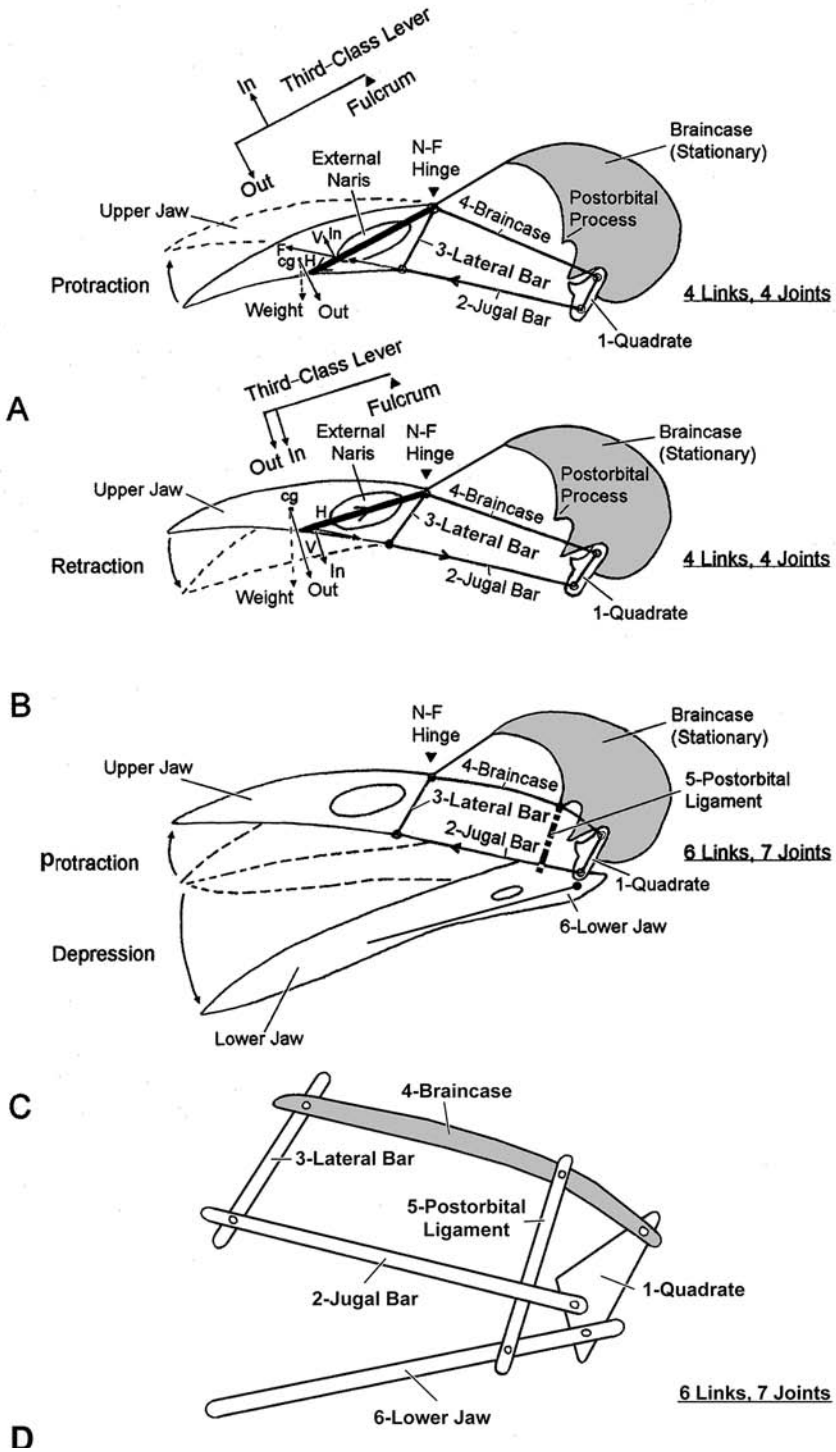


Figure 15.4. Diagrammatic analysis of lever mechanics of the prokinetic upper jaw of a crow. The rigid upper jaw is modeled as a beam (shown by the bold line) along the long diameter of the external naris. A–B, during protraction and retraction, the upper jaw acts as a third-class lever with a mechanism consisting of four links (numbered 1–4) and four joints (shown by circles) with a mobility 1. C, during jaw coupling by the postorbital ligament, the motions of the upper and lower jaws are dependent on one another. D, simplified representation of the coupled mechanism showing six links (numbered 1–6) and seven joints with a mobility 1.

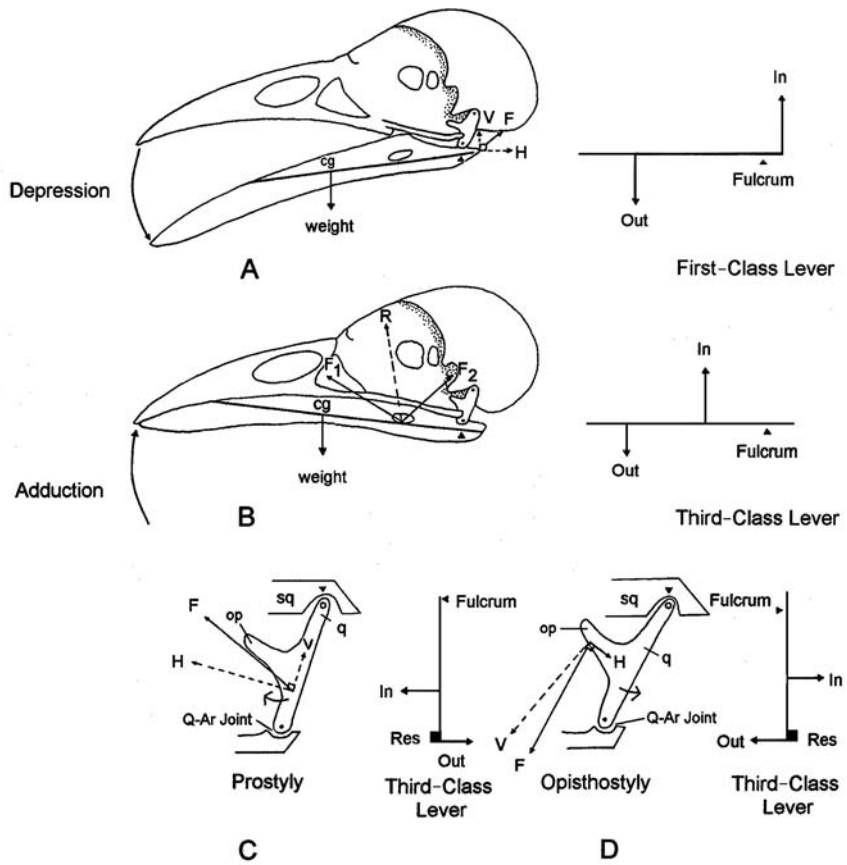


Figure 15.5. Diagrammatic analysis of the lever mechanics of the lower jaw and the quadrate of a crow. A, the lower jaw acts as a first-class lever during depression. B, during adduction, the lower jaw operates as a third-class lever. C–D, during prostylic (forward) and opisthostylic (backward) movement, the quadrate acts as a third-class lever. Abbreviations: cg, center of gravity; F, force; H, horizontal component of force; op, orbital process of quadrate; q, quadrate; Q-Ar Joint, quadrate-articular joint; R, resultant force; Res, resistance; V, vertical component of force.

bark or soft soil without full opening of the jaws to seize the food.

Because cranial kinesis is a three-dimensional mechanism, functional investigations must eventually include all dimensions. Yet, the kinematic study of avian skull is largely based on prokinesis and is restricted to two-dimensional analyses of forces exerted by the jaw muscles during feeding (Bock 1964; Bühler 1981; Zusi 1984, 1993; Zweers 1974). Jaw kinematics was formulated through postmortem manual manipulations or mechanical models rather than in vivo testing. Meekangvan et al. (2006) applied sophisticated nonlinear dynamic modeling tools to study avian kinesis that could be utilized to study the biomechanics of feeding and bite force as well as their effects on the frequency and modulation of bird songs. Similarly, Van Gennip and Barkhoudt (1992) attempted a three-dimensional kinematic computer model to understand the skull kinesis of birds. However, these complex quantitative models are difficult to apply in fossil forms where the skulls are often incomplete or badly crushed. In this discussion, two-dimensional analysis of kinematics of the upper jaw is investigated to trace the evolutionary history of cranial kinesis in birds. The position of the kinetic hinge, or the region of bending in the upper jaw integrated with other cranial features, is most pertinent in this study.

For simplicity, jaw movements can be differentiated into five integrated functional units for biomechanical

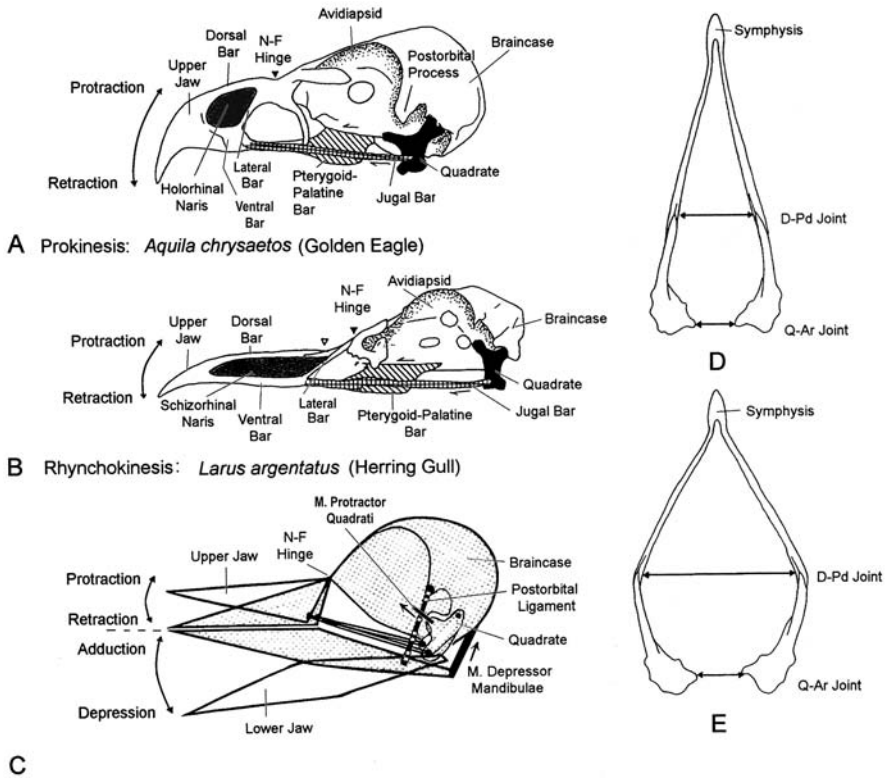


Figure 15.6. Two basic types of avian cranial kinesis. A, the holorhinal skull of a golden eagle in lateral view showing prokinesis. B, the schizorhinal skull of a herring gull in lateral view showing rhynchokinesis. The solid pointer indicates the nasal-frontal (N-F) hinge; the open pointer indicates the additional bending axis on the dorsal bar in rhynchokinesis; various movements of the jugal bar and the pterygoid-palatine bar are shown by arrows. C, schematic figure of the jaw coupling mechanism of a bird by the postorbital ligament in lateral view; stippled figure shows upper and lower jaws in closed position. D–E, mandibular spreading mechanism of herring gull during adduction (D) and depression (E) of the lower jaw in ventral view. Abbreviations: D-Pd joint, dentary-postdentary joint; N-F hinge, nasal-frontal hinge; Q-Ar joint, quadrate-articular joint.

analysis: (1) upper jaw, (2) quadrate, (3) lower jaw, (4) jaw muscles, and (5) postorbital ligaments (fig. 15.4D). The three bony units and the postorbital ligament are treated individually as rigid structures, each rotating about a fixed fulcrum; their movements can be analyzed separately using bone-muscle systems as levers (fig. 15.5C). In this analysis, it is important to identify the positions of the fulcrum (Δ), in-force or effort (In), and out-force or load (Out), on the lever arm during different phases of the cranial kinesis. Forces (F) are vector quantities. In this graphical analysis, either two forces are combined into one resultant (R) force, or a force is broken down into two components, horizontal (H) and vertical (V). This analysis differs considerably from that of Beecher (1962).

Upper Jaw Kinematics

The movement of the upper jaw is generated by a complex mechanism that includes the quadrates, pterygoids, palatines, jugal bars, and all associated muscles and ligaments. The closely associated pterygoids, palatines, and vomers are generally referred to as the pterygoid-palatine complex. Similarly, the jugal-quadratojugal unit is generally referred to as a jugal bar. These two bars—the pterygoid-palatine bar and the jugal bar—act as pushrod systems to transmit the force from the quadrate to the upper beak. Upper jaw mobility results from the movement of the quadrate and the pterygoid-palatine complex, which are powered by a set of muscles.

During the protraction cycle, the protractor muscles pull the quadrate and pterygoid-palatine bar forward, where the palatine slides along the parasphenoid rostrum, which acts as a guide or rail for the rostral movement. The sliding palatine pushes against the base of the upper jaw (vomer, maxilla, and premaxilla), resulting in rotation of the bill along the N-F hinge to open. In short, if the braincase is held stationary and the quadrates are swung forward, the upper jaw is raised. During the retraction cycle, the kinetic mechanism is reversed.

In the mechanism of protraction and retraction of the upper jaw, the quadrate is the vertical link and the main crank device. The head of the quadrate forms a fulcrum on the undersurface of the stationary braincase and moves forward and backward at its foot so that force can be transmitted to the beak through a pair of horizontal links. The jugal bar forms the lateral link, whereas the pterygoid-palatine acts as the medial link. The converging paired pterygoids meet nearly at the midline to couple there with the palatines. The quadrate is attached flexibly by "pin joints" to these horizontal links on either side of its foot that allow rotation at these joints so the anteromedial force can be executed during the elevation of the upper jaw, which is facilitated by several bending zones along the perimeter of the rostrum.

In modern prokinetic birds, the upper jaw is kinetically connected with the rest of the skull by three types of bending zones (Bühler 1981): one dorsally along the nasal-frontal (N-F or craniofacial) hinge zone, a pair laterally in the jugal bars, and a pair ventrally in the palatal bars (fig. 15.6A). In birds, the bending zones evolved in relation to the intimate fusion of the cranial elements and are usually recognized by an extreme flattening of the bone or multilayered sandwich-like structure. In rare cases, the craniofacial hinge is a true articulation (Zusi 1984).

In prokinesis, the upper jaw is inflexible and rotates around the nasal-frontal hinge. The upper jaw can be modeled as a rigid beam (Bock 1964, 1966), although the position of the beam is arbitrary. Since the external naris makes the upper jaw a rigid structure, the beam is drawn from the N-F hinge to the long diameter of the external naris. By changing the position of the beam and the angle of the jugal bar to the beak, the lever system of the upper jaw movement may vary from third order to second order (fig. 15.6 A, B).

Several devices, or "stops," limit protraction and retraction of the upper jaw. Protraction is limited mostly by soft parts (mainly ligaments) of the head. In some birds (e.g., crows), however, the orbital process of the quadrate abutting against the orbital wall acts as a bony stop to protraction. The bony structures that stop retraction are more widespread.

The Streptostylic Quadrate

The quadrate is a keystone of cranial kinesis, as it articulates with the squamosal (braincase), pterygoid, jugal, and mandible in flexible joints. Cranial kinesis is powered by the quadrate at the synovial otic joint so that the quadrate can move in a variety of directions relative to the fixed braincase. In streptostyly, the quadrate swings forward and backward as in squamates and birds; if the quadrate is fixed and immobile, as in other archosaurs, it is termed monimostylic (Versluys 1910). Monimostyly cannot generate cranial kinesis. Chatterjee (1991) has standardized the nomenclature of quadrate movement and coined several new terms to describe specific vectors. Streptostyly is divided further into two separate movements. In prostyly, the quadrate moves forward during protraction of the upper jaw (fig. 15.6C); in opisthostyly, the quadrate moves backward during retraction of the upper jaw at the rest position (fig. 15.6D). In parastyly, the quadrate moves sidewise in a transverse direction to mediate manidibular spreading. In most birds, quadrate movement is more complex than upper and lower jaw movement. During elevation of the upper jaw, the quadrate rotates not only rostrally but also medially toward the mobile pterygoid-palatine complex.

In birds, the dorsal head of the quadrate is expanded transversely to stabilize streptostylic movement. In most neognaths, the dorsal expanded head of the quadrate is further divided into two condyles that fit into a pair of concavities formed by the squamosal and prootic to form

a fulcrum, a transverse hinge, with the stationary braincase. This double ball-and-socket joint allows movement of the quadrate like a pendulum in propalinal motion without much lateral displacement. The orbital process of the quadrate serves as an effective lever arm for *M. protractor quadrati* during its forward movement. *M. protractor quadrati*, which originates on the medial wall of the interorbital septum and inserts on the dorsal surfaces of the pterygoid and quadrate bones, pulls the quadrate forward on its cranial fulcrum. In this mechanism, the horizontal (H) component is causing motion against the resistance (R) of the quadrate-articular (Q-Ar) joint; the quadrate thus acts as a third-class lever (fig. 15.6C). The backward movement of the quadrate is facilitated by *M. pseudotemporalis profundus*, which inserts on the tip of the orbital process and originates on the medial surface of the lower jaw. As this muscle contracts downward, it rocks the quadrate backward on its cranial fulcrum. The quadrate, in this mechanism, acts as a third-class lever (fig. 15.6D).

However, there are some independent and complex motions on the two sides of the skull, which are difficult to analyze. For example, some birds can move the quadrate units on the two sides somewhat independently. Similarly, motion of the upper and lower bills is generally confined to the vertical plane in most birds, but there are some exceptions where the jaw motions are far more complex. Furthermore, most birds show orthal motion of the mandible where the quadrate pivots on the articular; however, some birds develop propalinal motion where the mandible can slide in relation to the upper beak for skilled manipulation. Some birds can move the upper and lower bills independently; in other birds, motion of the upper jaw during kinesis is coupled to lower jaw motions. Streptostylic quadrate movement facilitates movement of the upper jaw, whereas parastylic quadrate movement allows intramandibular bending of the lower jaw (Chatterjee 1991). A wide range of morphological variation among various kinetic units such as the bills, the jugal bar, the quadrate, and the pterygoid-palatine bar indicates the diversity of avian cranial kinesis that may be linked to different feeding behavior (Zusi 1993).

Lower Jaw Kinematics

The articular of the lower jaw is attached to the quadrate of the skull at a double ball-and-socket joint. The jaw joint permits the lower jaw to rotate dorsoventrally and lateromedially and to slide back and forth on the quadrate. The universal movement of the lower jaw is opening (depression) and closing (adduction) in orthal fashion in which the whole mandible is rotated about the quadrate-articular (Q-Ar) joint (fig. 15.6A, 15.6B). In addition, some birds developed lateromedial flexibility of the lower jaw (mandibular spreading) for food manipulation. Although the lower jaw bones are fused in birds with a bony symphysis, many birds develop two pairs of flexion zones within the ramus: one at the mid-length of the mandible, between the dentary and postdentary (D-Pd) bones, the other at the quadrate-articular (Q-Ar) joint (fig. 15.5D, E) (Bühler 1981).

M. pterygoideus pulls the medial process of the lower jaw forward, causing the D-Pd joint and Q-Ar joint to bow outward during depression of the lower jaw (fig. 15.5D, E). Mandibular spreading (streptognathism) allows birds to increase the diameter of the throat for swallowing large objects. It also permits them to feed their young with the chick's head inside the mouth (Bühler 1981). The mechanism apparently evolved from the intramandibular kinesis of theropods. Some birds can move the lower jaw backward (opisthokinesis) assisted by the opisthostylic quadrate in a propalinal (gliding) fashion. This mechanism allows shifting of food backward toward the throat by mandibular raking.

In the movement of the lower jaw, the hinge lies at the quadrate-articular joint. The jaw is opened by the constriction of *M. depressor mandibulae*, which originates at the ventrocaudal edge of the braincase and inserts on the retroarticular process of the lower jaw. Contraction of this muscle pulls the retroarticular process up, causing the tip of the lower jaw to fall. During depression of the lower jaw, the in-force and out-force are in opposite directions on either side of the fulcrum so that the lower jaw operates as a first-class lever (fig. 15.6A). The main adductor muscles for closing the jaw are *M. pterygoideus*,

M. adductor mandibulae, and *M. pseudotemporalis profundus* acting together as a dorsally directed force. These muscles attach to the front and rear sides of the braincase and to the lower jaw in front of the quadrate (fig. 15.7).

Jaw Muscles in Cranial Kinesis

The jaw mechanism of birds is powered by the jaw muscles and directed by the articulations, ligaments, and flexible bony hinges (Bühler 1981). Protractor and retractor muscles are key structures involved in cranial kinesis that help to move the palatoquadrate complex independently of the braincase and mandible. One of the primary muscles for the forward movement of the quadrate is *M. protractor quadrati*, which attaches to the interorbital septum of the braincase and to the medial side of the quadrate and pterygoid. The action of *M. protractor quadrati* on the orbital process pushes the foot of the quadrate forward. The forward movement of the quadrate sets in motion a chain of events leading to the protraction of the upper jaw. As the quadrate foot moves forward, this force is imparted to the jugal bar laterally and pterygoid medially, which, in turn, rotates the upper jaw along the flexible N-F hinge and raises the beak. The palate also is detached from the braincase, making the upper jaw movement independent of the braincase.

The reverse action of the quadrate system retracts the upper jaw. The action of *M. pseudotemporalis profundus* on the quadrate pushes the foot of the bone backward. In retraction, another muscle, *M. pseudotemporalis profundus*, which attaches to the lateral side of the quadrate and to the medial side of the mandible, acts in opposition to *M. protractor quadrati*. *M. pseudotemporalis profundus* pushes the quadrate foot backward, resulting in the pulling of the jugal bar and the upper jaw downward (fig. 15.7). This action in turn, pulls the jugal bar and pterygoid-palatine bar caudally. Jaw closing muscles (*M. pterygoideus* and adductors) act in opposite fashion to move the beak downward to grasp food, and return the kinetic mechanism to the rest position. As a result, the upper jaw is retracted. Other cranial muscles may also be involved in this movement (Zweers 1974).

The primary muscle in depression of the lower jaw is *M. depressor mandibulae*, which attaches to the rear of the braincase and to the caudal part of the lower jaw. Contraction of this muscle pulls the rear of the lower jaw up, causing the tip to move downward. Three jaw muscle groups, *M. pterygoideus*, *M. adductor mandibulae*, and *M. pseudotemporalis profundus*, all contribute to the adduction of the lower jaw (fig. 15.7).

The Postorbital Ligament and Jaw Coupling

In many birds, a strong postorbital ligament has an important role in cranial kinesis and jaw coupling. Some birds lack the postorbital ligament and the jaws are uncoupled; they can move the upper and lower jaws independently. In other birds (e.g., zebra finch), the postorbital ligament is present, but it is slack and does not block the depression of the lower jaw (Nuijens and Bout 2000). However, in most recent birds, the upper and lower jaws are coupled in such a fashion that there is a mechanical linkage between the elevation of the upper jaw and the depression of the lower jaw (Bock 1964). In this model, the motions of the upper and lower jaws are dependent on one another during the opening cycle. Typically, the postorbital ligament, when loaded by muscle action, mediates such jaw coupling. This ligament runs from the ventral tip of the postorbital process of the braincase to the external process of the lower jaw anterior to the quadrate's articulation in such a way that it restricts the depression of the mandible. Several mechanical hypotheses have been proposed to explain coupled kinesis, including the presence of stiff ligaments between the skull and mandible (Bock 1964), an interlocking jaw joint (Bock 1964; Zusi 1967), and simultaneous activity of jaw-opening and jaw-closing muscles (Bühler 1981). The postorbital ligament is taut and inextensible, is made of collagen, and joins the postorbital process with the external process of the lower jaw (Van Gennip and Barkhoudt 1992; Gussekloo et al. 2001).

The stiffness of the postorbital ligament is responsible for jaw coupling. It can be measured by the ratio of stress to strain, called the Young's modulus of elasticity, which is about 1,500 MPa; its extensibility is 0.1 (Vogel 2003), indicating that this ligament is relatively stiff during jaw movement and functions like a bony bar. Since the postorbital

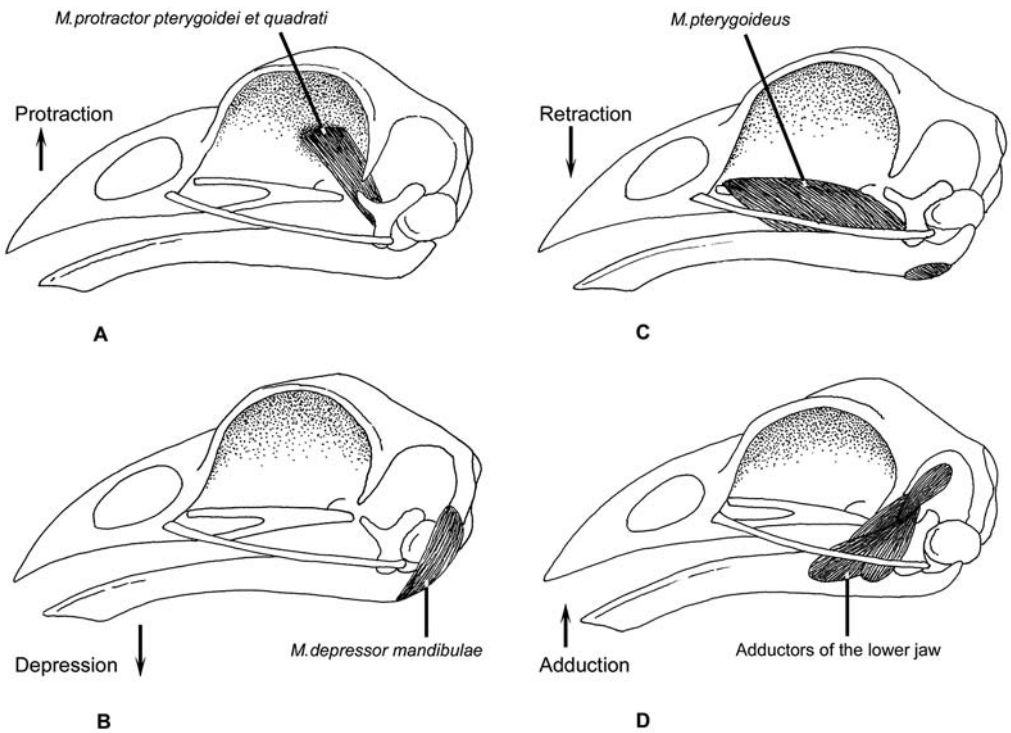


Figure 15.7. Simplified avian jaw muscles. A, *M. protractor quadrati* for forward movement of the quadrate; B, *M. depressor mandibulae* for the lower jaw opening; C, *M. pterygoideus* for backward movement of the quadrate; D, adductor muscles for the lower jaw closing.

ligament lies close to the jaw joint, by mechanical demand it has to be stiff and taut to be effective for jaw coupling. Several recent experiments with the postorbital ligaments suggest that this ligament is unstretchable in most species of birds and has a locking mechanism for the lower jaw, which prevents its depression (Van Gennip and Barkhoudt 1992; Gussekloo et al. 2001). Alexander (1983) modeled the postorbital ligament in birds as a rigid link. According to him, the postorbital ligament has a similar effect on the skull mechanism as if it were an additional bony bar, hinged to the braincase and lower jaw. The whole skull is then converted into a mechanism of six links and seven joints incorporating the postorbital ligament and lower jaw in the system, as shown in figure 15.4D.

In the jaw-coupling mechanism (Bock 1964), the postorbital ligament must be placed in tension before the upper and lower jaws can be physically locked during jaw opening. If the postorbital ligament were flexible, slack, and highly stretchable, jaw coupling in birds would not work (Gussekloo et al. 2001). To understand the role of the postorbital ligament in jaw coupling, we have made a simple wooden model with six links and seven joints, and used various materials (rubber string, cotton string, nylon string, and thin steel strap) to simulate the postorbital ligament. Of these elastic materials we found that the steel strap, which is fairly rigid, works very well as a proxy to the postorbital ligament in our model (fig. 15.8) to initiate the chain of events of jaw coupling during the opening and closing of the jaws, confirming the kinematic action predicted by Bock (1964).

When the jaw is closed, the jaw joint (quadrate-articular joint) is situated caudally proximate to the insertion of the postorbital ligament on the mandible (fig. 15.8A-C). As soon as the jaw begins to open upon contraction of the depressor mandibulae, the stiff postorbital ligament becomes taut, locking the lower jaw. This causes the mandibular attachment of the postorbital ligament to slide slightly forward relative to the attachment on the stationary braincase, which in turn pushes the quadrate forward and raises the upper jaw. The rostral movement

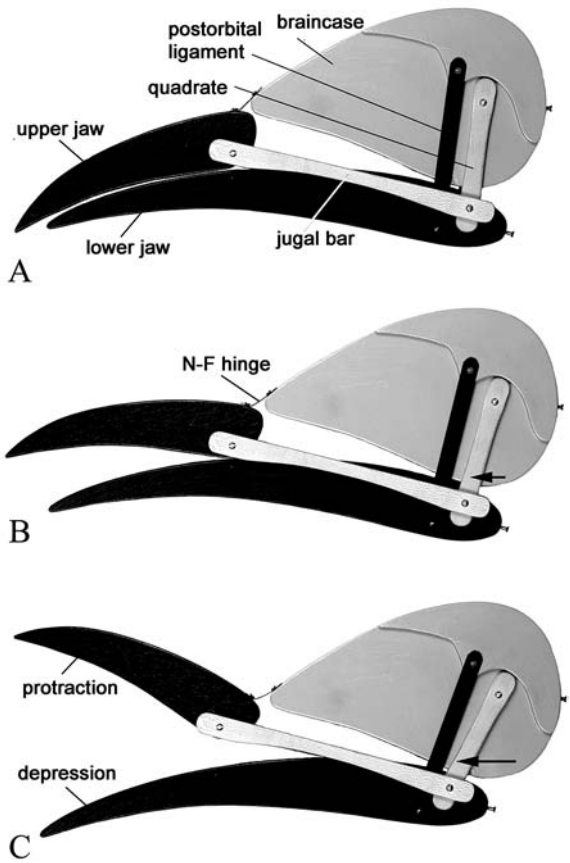


Figure 15.8. Diagram illustrating the principle of coupled kinesis outlined by Bock (1964). A, both jaws are closed by the stiff postorbital ligament. B, the upper jaw begins to protract as the quadrate is pushed forward (shown by arrow). C, as the upper jaw is fully elevated, the postorbital ligament slackens and the lower jaw is depressed.

of the quadrate slackens the postorbital ligament and unlocks the lower jaw, which begins to depress. As the jaw is depressed, the quadrate is swung forward to push the jugal and pterygoid-palatine bar forward, raising the upper jaw. There is a mechanical coupling between the lowering of the mandible with the raising of the upper jaw in birds, orchestrated by the streptostylic quadrate and the stiff postorbital ligament. In reverse, the quadrate must swing backward during jaw closing.

In this jaw-coupling mechanism, the depression of the lower jaw is possible only when the upper jaw is elevated, but the mandible cannot be depressed without the upper jaw being raised (Bock 1964). Various experiments suggest that the action of *M. depressor mandibulae* may also to serve swing the posterior end of the lower jaw up, pushing the quadrate forward and therefore raising the upper jaw (Zusi 1967; Hoese and Westneat 1996). During the closing cycle, when the adductor muscle raises the lower jaw, it slackens the postorbital ligament but does not force the upper jaw down. The upper jaw is restricted when the quadrate is swung backward to occlude the lower jaw (fig. 15.8). The postorbital ligament does not transmit forces during jaw closing.

Origin and Evolution of Cranial Kinesis

Cranial kinesis in extant tetrapods is rare, being restricted to just two major clades, squamates and birds. The dinosaur skull has long been of interest to paleobiologists in studying potential cranial kinesis (Versluys 1910; Bakker 1986; Mazzetta et al. 1988; Rayfield 2004), but preservational problems and lack of morphological correlates prevent detailed analysis of kinesis of this group. Since nonavian theropods retained an intact diapsid arch and monimostylic quadrate, Chatterjee (1991, 1997) concluded that the theropod skull was largely akinetic because many of the avian kinetic joints show firm contacts in theropod skulls, prohibiting any movement. However, lower jaw mobility along the intramandibular joint is possible in theropods with the parastylic quadrate that allowed the caudal part of the mandible to flex sidewise (Bakker 1986).

Holliday and Witmer (2008) critically reviewed various hypotheses of cranial kinesis in different groups of nonavian dinosaurs and suggested four criteria necessary but individually insufficient for the inference of cranial kinesis: (1) synovial otic joints, (2) synovial basal (basipterygoid) joints, (3) protractor muscles, and (4) permissive kinematic linkages (fig. 15.4A). They suggested that powerful protractor musculature such as protractor and pterygoideus muscles were present in most nonavian dinosaurs, indicated by their osteological correlates such as preotic and levator pendants in the braincase. They pointed out that intracranial synovial joints such as the otic and basal joints are necessary to allow kinetic movement, and protractor muscles would drive the system. Nonavian dinosaurs achieved the first three criteria,

which is not surprising because these features are diapsid plesiomorphies and were only partially kinetically competent. However, according to Holliday and Witmer, the most important component for achieving cranial kinesis is the kinematic linkage system, which is lacking in dinosaurs. This linkage system would have permitted mobility of the upper jaw. Thus dinosaurs, including nonavian theropods, were not functionally kinetic.

In contrast, all modern birds possess a streptostylic quadrate, a powerful morphological correlate to detect kinesis (Bock 1964). Avian cranial kinesis is powered by the streptostylic quadrate, where the anteromedial force is transmitted to the base of the upper jaw by two push-rod systems: the jugal bar and the pterygoid-palatine bar. The maxilla, jugal, and quadratojugal are reduced to a rod-like structure, the jugal bar. In the palate, a sliding contact is established between the lacrimal and the jugal bar. Similarly, the pterygoid-palatine bar has become mobile with the loss of the ectopterygoid and epipterygoid bones, along with the development of a flexible joint between the pterygoid and the quadrate. The basipterygoid articulation is loose and reduced, which increases the range of movement of the pterygoid-palatine bar. Free mobility of the jugal bar and the pterygoid-palatine bar is essential in avian kinesis. In nonavian dinosaurs many bony stops prevent the mobility of the quadrate, the jugal bar, and the pterygoid-palatine bar. Without quadrate streptostyly, the essential kinematic linkages cannot be achieved.

Chatterjee (1991, 1997) discussed several blocking structures in nonavian theropods that prevent streptostyly and the sliding action of the jugal and pterygoid-palatine bars. For example, the quadrate is bound to the quadratojugal by a long immovable suture and to the palate by a deep overlap of the pterygoid. Furthermore, two vertical bars of the lower temporal opening—the squamosal-quadratojugal bar and the postorbital-jugal bar—act as bony stops in front of the quadrate, thereby preventing streptostyly and sliding of the jugal bar. Similarly, the transverse ectopterygoid bone that connects the palate with the jugal and the epipterygoid that ties the palate with the undersurface of the skull roof are effective bony stops that make the pterygoid-palatine bar immobile. Without the elimination of these bony stops, nonavian theropods could not achieve cranial kinesis.

The following osteological correlates are necessary for inferences of cranial kinesis in nonavian theropods and early birds (Bock 1964; Bühler 1981; Chatterjee 1991, 1997; Holliday and Witmer 2008): (1) the ball-and-socket joint of the quadrate head with the squamosal with the development of streptostyly; (2) loss of the squamosal-quadratojugal bar; (3) loss of the postorbital-jugal bar; (3) loss of the ectopterygoid; (4) loss of the epipterygoid; (5) development of the orbital process in the quadrate; (6) the pin joint between the quadrate and the quadratojugal; (7) the pin joint between the quadrate and the pterygoid, ventral to the orbital process; (8) the reduced basal joint between the pterygoid and the basipterygoid process; (9) the craniofacial hinge joint between the nasal and the frontal; (10) the lateral bending zone in the jugal bar; and (11) the ventral bending zone in the palatal bar.

Birds acquired streptostyly and kinesis by the loss of these bony stops, including the anterior, dorsal, and posterior bars of the lower temporal arcades, so that the orbit becomes confluent with the upper and lower temporal fenestrae. This modified diapsid configuration of the temporal region, the avidiapsid condition, is a powerful morphological correlate to infer the presence of cranial kinesis (Chatterjee 1991). All modern birds possess this avidiapsid condition and kinetic skull. In nonavian dinosaurs, the diapsid arches remain intact, indicating the akinetic condition.

Holliday and Witmer (2008) concluded that most nonavian theropods possessed synovial basal and otic joints but lacked true kinesis as seen in birds. They suggested that these synovial joints might simply be cartilaginous sites that facilitated cranial growth during ontogeny. Other than growth, these synovial joints may be linked to feeding behavior. All nonavian theropods had a fixed quadrate (strong quadrate-pterygoid and strong squamosal-quadrate joints) and akinetic skulls with intact diapsid arches. They had a more mechanically robust skull architecture than birds with a streptostylic quadrate and a kinetic skull. Bite performance should be an important

driving factor for the retention of an akinetic skull with a monimostylic quadrate in nonavian theropods. However, hard biting puts considerable stress on the quadrate and the epipterygoid and on their connections with the rest of the skull. Reducing these bony connections with the inception of streptostyly might be one of the biomechanical solutions for reducing the joint forces in the skull of birds at the expense of decreased skull robusticity. From an evolutionary perspective, birds traded intracranial mobility and reduced buccal apparatus for the robust skull of nonavian theropods by changing their feeding behavior so that mastication is transferred from the mouth to grinding gizzards. Birds use their bills for procuring food, not for chewing and processing, and these delicate and flexible bills can excel at this role. Many of the anatomical modifications along with cranial kinesis include tooth reduction, acquisition of a horny beak, the reduction of complex jaw musculature, the reduction of the tongue, and the reduction of the cephalic alimentary canal, all possibly evolved in response to lightening the avian body for flight.

However, cranial kinesis did not start at the avialan node but took millions of years of experimentation, swinging back and forth from the akinetic to the kinetic condition among different lineages of maniraptorans. We see the beginning of this trend of reduction of the bony struts of diapsid arches in some maniraptorans such as alvarezsaurids and oviraptorosaurs. Chiappe et al. (1998) described a juvenile alvarezsaurid skull *Shuvuuia* where the orbit becomes confluent with the lower temporal opening with the loss of the postorbital process of the jugal and of the squamosal process of the quadratojugal, resulting in the formation of a slender jugal bar and a double-headed and mobile quadrate. In this configuration, the orbit is confluent with the lower temporal fenestra, but the upper temporal arch is still intact. Chiappe et al. suggested that the quadrate in *Shuvuuia* achieved streptostyly to initiate prokinesis (fig. 15.9A). Holliday and Witmer (2008) were skeptical about the intracranial ability of *Shuvuuia* because of uncertainties of several osteological correlates such as the development of lateral and palatal bending zones and the loss of the ectopterygoid. Moreover, the nasofrontal zone is complex and rigid, prohibiting any flexion. However, they concurred that *Shuvuuia* displays some of the key features of the avian kinetic system, probably an early form of kinesis. The mobility of the quadrate bone in *Shuvuuia* weakens skull robusticity but can reduce the joint forces acting on the skull and provide a shock-absorbing function during feeding. The primitive kinesis in *Shuvuuia* may be an ontogenetic feature. The skull of an adult alvarezsaurid theropod represented by *Haplocheirus* from the Late Jurassic of China shows an intact diapsid configuration without any hint of kinesis (Choiniere et al. 2010).

Another group of maniraptorans shows a similar trend. Oviraptorosaurs are often regarded as a sister group of avialans (Maryanska et al. 2002; Xu et al. 2002, 2011). The skulls of oviraptorosaurs show various avian attributes, including an enlarged, beaked premaxilla, a reduced maxilla, highly pneumatized skull bones, a large external naris, a slender jugal bar, and a fused mandibular symphysis (fig. 15.9B). The palate is highly modified such that the ectopterygoid is vertical and connects the lacrimal to the palatine. The pterygoid-basisphenoid contact is loose, indicating retention of the basal synovial joint (Osmolska et al. 2004). An isolated quadrate, possibly belonging to a juvenile individual, is distinctly avian with the development of a double-headed quadrate for contacts with the squamosal and the braincase, a lateral quadratojugal cotyle, and a medial pterygoid condyle (fig. 15.9C) (Maryanska and Osmolska 1997). Most likely, the quadrate achieved a synovial otic joint in the juvenile stage in oviraptorosaurs, but became monimostylic in the adults as it fused with the pterygoid. A juvenile skull of *Caudipteryx* strengthens this observation that ontogeny modifies cranial kinesis (Zhou et al. 2000). In this specimen, the spherical head of the quadrate fits into a cotyle of the squamosal in a ball-and-socket joint, suggesting the development of a synovial otic joint. Moreover, it appears that there was some reduction in the articulations of the vertical bars of the diapsid arches to achieve the early stage of kinematic linkages and streptostyly: loss of contact between the squamosal and the quadratojugal and between the postorbital and the jugal, resulting in the

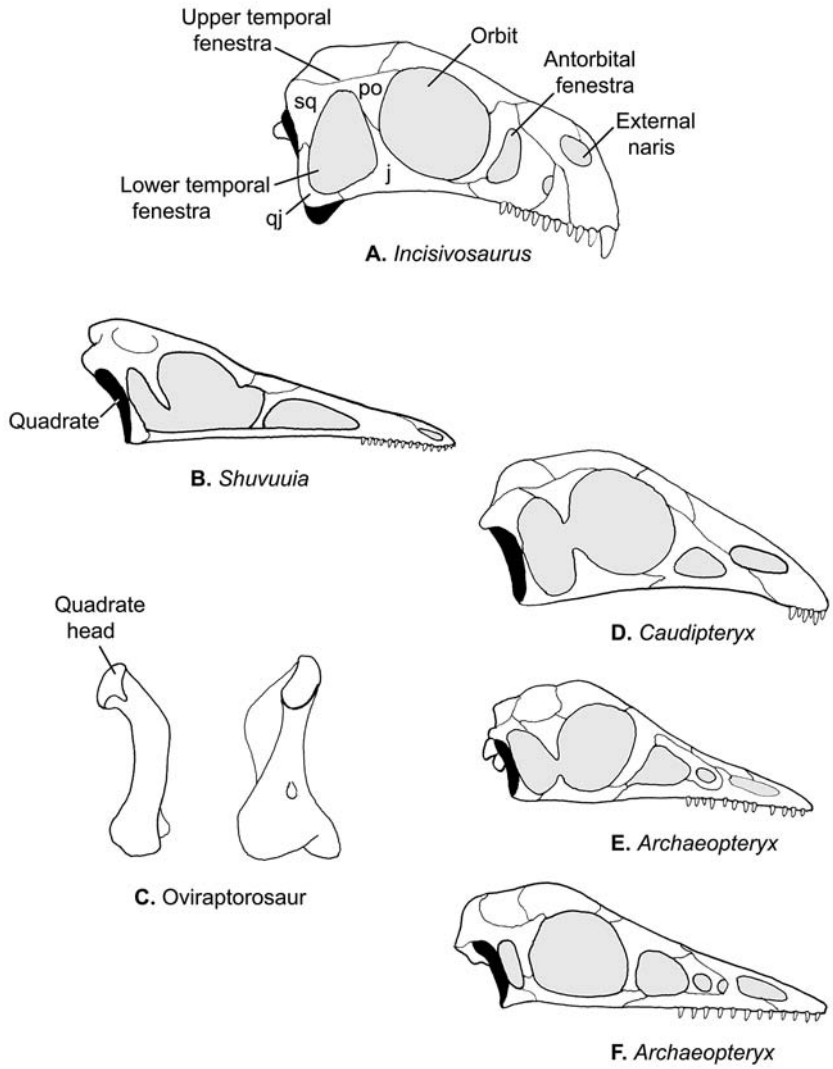


Figure 15.9. Several maniraptoran theropod skulls showing the beginning of permissive kinematic linkages from the primitive diapsid temporal configuration during ontogeny. A, an adult skull of an oviraptorosaur *Incisivosaurus* from the Early Cretaceous of China with intact diapsid arches and monimostylic quadrate (Xu et al. 2002). B, *Shuvuuia*, a juvenile alvarezsaurid theropod from the Late Cretaceous of Mongolia probably developed the beginning of kinesis with the loss of the descending process of the squamosal and bird-like jugal bar (Chiappe et al. 1998). C, lateral and posterior views of an isolated right quadrate of an oviraptorosaur, probably belonging to a juvenile individual of *Ingenia* or *Conchoraptor*, showing a distinct quadrate head and the development of synovial otic joint; however, the quadrate becomes fused with the squamosal and quadratojugal in adult oviraptorosaurs (Maryanska and Osmolska 1997). D, *Caudipteryx*, a juvenile oviraptorosaur from the Early Cretaceous of China showing reduction of the squamosal-quadratojugal bar and the postorbital-jugal bar (modified from Zhou et al. 2000). E, juvenile *Archaeopteryx*, Eichstätt specimen with modified diapsid condition, where the postorbital process of the jugal is lost so that the orbit becomes confluent with the lower temporal opening (Chatterjee 1997). F, adult *Archaeopteryx*, London specimen, with intact diapsid arches, where the postorbital-jugal bar appears to be complete (Paul 2002). In the evolution of cranial kinesis, with the reduction or loss of the squamosal-quadratojugal bar and the postorbital-jugal bar, the quadrate (shown in black) becomes streptostylic. From these examples, it appears that maniraptoran theropods might have some flexibility in the skull bones in the juvenile stages, but the joints become rigid in adults, an example of the heterochronic evolution of cranial kinesis. Presumably, the diapsid arches are developed during growth, making the skull akinetic. The discordance between phylogeny of early birds and the suggested path of cranial kinesis evolution may indicate recurrent heterochronic events.

formation of a slender jugal bar (fig. 15.9D). The frontonasal joint seems to be an overlapping and sandwich-like precursor to craniofacial flexion. However, in adult specimens of oviraptorosaurs, these contacts of vertical bars are reestablished and the skull becomes akinetic with the development of a monimostylic quadrate (fig. 15.9C). Even then, all the diapsid arches are considerably slender and rod-like in oviraptorosaurs, indicating potential loss of bite force compared to that of other nonavian theropods. Both oviraptorosaurs and alvarezsaurids suggest that juvenile maniraptorans developed some form of intracranial mobility perhaps to facilitate cranial growth and absorb shock during feeding; however, they lost kinesis in their adult stages with changing food habits (Holliday and Witmer 2008). Modern birds offer some clue to this behavioral change during ontogeny: nearly all seed-eating birds start their newly hatched young on insects, then gradually switch them to a vegetable diet.

The Role of Heterochrony in Cranial Kinesis

Heterochrony, or changes in the timing or rate of developmental events relative to the ancestral condition, has played a significant role in the evolution of cranial kinesis in birds, particularly in the reduction of diapsid arches. In recent years, many paleontologists have used heterochrony as a working hypothesis to account for the phylogenetic changes in many lineages of invertebrate evolution to assess whether a particular species is either peramorphic or paedomorphic; however, understanding which process or processes caused the heterochronic changes is more difficult (McKinney and McNamara 1991; McNamara 2001). Unlike invertebrates, where the fossil record is usually dense and represents many stages in developmental and evolutionary pathways, the ontogenetic data on fossil vertebrates, especially on nonavian theropods and Mesozoic birds, are sparse. Because of this deficiency, the role of heterochrony in the evolution of birds has received minimal attention in recent years, and has focused primarily on arguments concerning the paedomorphic development of palaeognaths (de Beer 1958; James and Olson 1983; Livezey 1995). Thulborn (1985) briefly identified the following neotenic features in *Archaeopteryx* retained from its theropod ancestors: very large orbits, an inflated braincase, and reduction in the number of teeth. However, if birds had simply reduced adult size by becoming paedomorphic, as is commonly believed (Alberch et al. 1979), they would have retained only juvenile traits at this reduced adult size. However, in adult birds both paedomorphic and peramorphic features reappear. For example, they show the derived development of many traits in the skeleton, including the peramorphic development of wings and an increase in skeletal fusion of many elements (Padian et al. 2001). The evolution of birds is more complex and arose by heterochronic tradeoffs—by mixing paedomorphic and peramorphic traits at different phylogenetic levels (see chapter 11). The evolution of cranial kinesis suggests similar dissociated heterochrony.

Current lack of ontogenetic data in the skulls of most taxa of Mesozoic birds and their theropod antecedents hampers the analysis of the role of heterochrony in the cranial kinesis evolution of birds. Modern birds differ from their maniraptoran relatives with the loss of certain bones and bony processes. Among these are the postorbital, the postorbital process of the jugal, the jugal process of the postorbital, the squamosal process of the quadratojugal, the quadratojugal process of the squamosal, the pterygoid process of the quadrate, the ectopterygoid, the epipterygoid, and the coronoid of the mandible. In addition, the cranial bones are fused in modern birds but retained distinct sutures in avialans. This pattern of loss of bones and bony processes (which are present in nonavian theropods) and fusion of cranial bones appears to reflect an overall trend in peramorphosis within birds for acquisition of cranial kinesis, in contrast to the original predominantly paedomorphic origination of birds from nonavian theropods.

In juvenile *Shuvuuia* and *Caudipteryx*, the jugal has not established contact with the quadratojugal, as seen in the embryonic *Sphenodon* (Rieppel 1993) and the juvenile Eichstätt *Archaeopteryx* (Chatterjee 1991), but appears to have a complete postorbitojugal bar in the adult London specimen (fig. 15.9E, F) (Paul 2002). The descending process of the squamosal in front of the quadrate and the

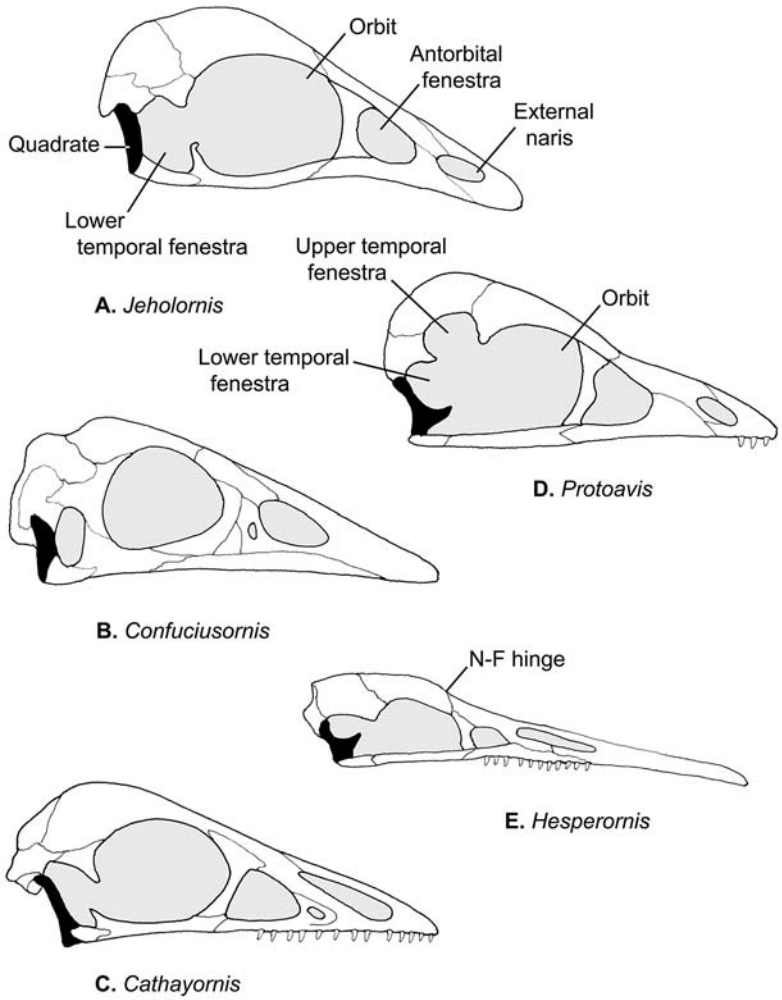


Figure 15.10. Modifications of temporal configuration in some Mesozoic birds. A, *Jeholornis*, a primitive avialan from the Early Cretaceous of China with modified diapsid arches; B, *Confuciusornis*, a pygostylian bird from the Late Cretaceous of China with intact diapsid arches (modified from Chiappe et al. 1999); C, *Cathayornis*, an enatiornithine bird from the Late Cretaceous of China probably developed streptostyly and primitive kinesis with the breakdown of the squamosal-quadratojugal bar, the pin joint between the quadrate and the quadratojugal, and the lender jugal bar (modified from Paul 2000); D, *Protoavis* from the Late Triassic of Texas has developed an avidiapsid condition, streptostylic quadrate, and primitive prokinesis; E, *Hesperornis*, an ornithurine bird from the Late Cretaceous of Kansas, has developed primitive prokinesis with a flexible craniofacial hinge.

presence of the ectopterygoid imply that the quadrate could not swing forward in *Archaeopteryx*. Perhaps *Archaeopteryx* developed some degree of backward mobility, or opisthostyly, to shift the mandible for raking food (Chatterjee 1991, 1997).

Avian cranial kinesis begins to develop in early avialans such as *Jeholornis*, with the modification of temporal configurations as seen in *Shuvuuia*, where the orbit and the lower temporal opening become confluent (Zhou 2004). Moreover, the bony strut in front of the quadrate, the squamosal-quadratojugal, is lost to make the quadrate streptostylic (fig. 15.10A). The beginning of kinesis in the skull of *Jeholornis* might be linked to new food preferences such as seeds as revealed from stomach contents (Zhou and Zhang 2002). The large number of undigested and intact ovules suggests that the bird swallowed them whole, to be digested in the gizzard, but they have been preserved in a large crop in the anterior part of the stom-

ach before its death. It seems that *Jeholornis* had a paedomorphic maniraptoran skull during the initial breakup of diapsid arches as seen in *Shuvuuia*.

In contrast, *Confuciusornis* (fig. 15.10B) seems to have intact diapsid arches with a robust postorbitojugal bar and monimostylic quadrate, probably representing a paedomorphic reversal (Chiappe et al. 1999). Moving up from *Confuciusornis* on the cladogram of birds, we come to enantiornithine birds such *Cathayornis* that retained an early stage of cranial kinesis as in *Jeholornis* with an incomplete lower temporal arch in which the orbit becomes confluent with the lower temporal opening (fig. 15.10C). Here, the descending process of the squamosal is lost in front of the quadrate and the quadratojugal has developed a pin joint with the quadrate to make it streptostylic. Most likely, the lacrimal slid against the rod-like jugal bar during prokinesis.

The next stage of modification of the temporal configuration is found in *Protoavis*, where the orbit becomes confluent with both upper and lower temporal openings with the breakdown of diapsid arches (fig. 15.10D). The quadrate develops streptostyly with a ball-and-socket otic joint. A prokinetic joint is developed in front of the orbit between nasal and frontal bones. The loss of the upper temporal arcade in *Protoavis* may represent a peramorphic trend since it is retained in *Jeholornis* and oviraptorosaurs. Thus peramorphosis may be responsible for the evolution of the avidiapsid condition in *Protoavis* and ornithurine birds from their nonavian ancestors with the loss of diapsid arches.

Cranial kinesis must have developed very early in avian evolution as documented by the oldest Triassic bird *Protoavis* (Chatterjee 1991). Like recurrent flightlessness, cranial kinesis was lost several times during its basal radiation, and most avialans, pygostylians, and enantiornithine birds retained akinetic skulls. Even the flightless ratites have considerably reduced the degree of cranial kinesis in comparison to their neognath counterparts. Why and how did birds experience this reversal? Ironically, the very process that contributed to the evolution of cranial kinesis in birds has also resulted in the loss of kinesis. The presence of a primitive form of kinesis in *Shuvuuia*, *Caudipteryx*, *Archaeopteryx*, and *Protoavis* indicates that the akinetic skull of *Confuciusornis* may represent reversal, the secondary loss of kinesis by paedomorphism. Although there is a complex interplay of paedomorphism and peramorphism in the early evolution of birds, peramorphism may be a dominant factor in the evolution of avian cranial kinesis in modern birds from akinetic theropod ancestors, a major adaptive breakthrough that led them to exploit a wide range of feeding habits in concert with flight.

From the *Protoavis* condition, the kinematic linkages have attained a stable configuration with the appearance of ornithurine birds such as *Ichthyornis* and *Hesperornis* with a flexible craniofacial hinge. In modern birds, the mobility of the jaw apparatus is further refined with the fusion of bones and development of highly flexible joints, loss of teeth, a movable pterygoid-palatine joint, and the acquisition of a postorbital ligament and jaw coupling (fig. 15.10E).

Heterochrony has played a role in the remodeling of modern bird skull architecture. For example, palaeognathous birds show paedomorphic retention of cranial sutures, a juvenile condition found in living birds (fig. 15.11A). The sutures are lost in adult neognaths. Similarly, the presence of basipterygoid processes in ratites, as in nonavian theropods, appears to be another paedomorphic feature, which is lost in neognaths by peramorphism. In some adult neognathous birds, such as chickens (and other gamebirds), some storks, and cockatoos, an upper temporal opening appears (Heilmann 1926; Bellairs and Jenkin 1960). In these birds, the postorbital process (formed by the frontal and laterosphenoid) and the zygomatic process of the squamosal contribute to the ventral arch of the upper temporal opening (fig. 15.11B–D). This separate upper temporal opening is not present in the skull of the young chicken (Jollie 1957) or adult specimens of most other bird species and must be a heterochronic development. However, this upper temporal opening is not homologous to the corresponding opening of nonavian theropods or early avialans because in these early diapsids the squamosal and postorbital bones frame the diapsid arch ventrally. In modern birds, the postorbital bone is lost; the frontal and the laterosphe-

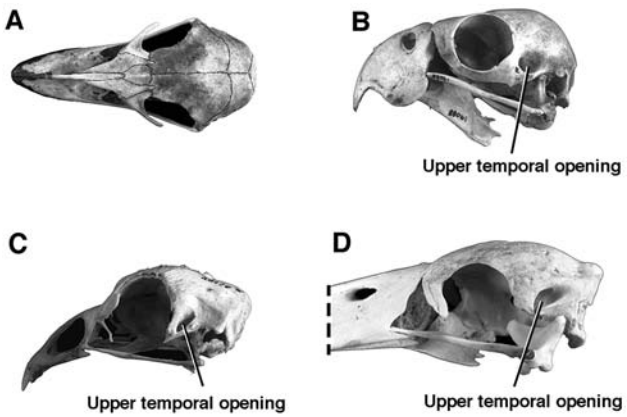


Figure 15.11. A, dorsal view of the skull of an adult individual of *Emu* showing paedomorphic retention of cranial sutures. B, C, and D, peramorphic development of the upper temporal opening in some modern birds such as the cockatoo (*Cacatua*), the chicken (*Gallus*), and the stork (*Leptoptilos*).

noid contribute to the postorbital process, which joins with the squamosal to form this upper temporal arcade. Most probably the new upper temporal opening in these modern birds is a peramorphic feature, a new innovation associated with changes in the relationships of the adductor muscles, which take their origin from this site.

Modification of the Avian Skull

The avian skull is modified greatly from the ancestral paravian design in response to cranial kinesis. However, patterns of bone loss and gain, particularly in relation to bars and fenestrae of diapsid configuration during ontogeny and phylogeny, and the degree of streptostyly have complicated the issue of the origin of avian cranial kinesis, especially in early avialans.

There are four critical areas where profound architectural changes signal permissive kinetic linkages: temporal configuration, quadrate morphology, palatal structure, and the external naris (Chatterjee, 1991, 1997). Using maniraptoran design as the starting point, the predicted sequence of cranial evolution in birds can be reconstructed.

Modification of the Diapsid Temporal Configuration

Birds arise from a diapsid ancestry, but they show considerable modification of the skull pattern in response to cranial kinesis. The braincase is much inflated and ossified with the skull roof to form a stationary unit in response to movable jaws. The jaws are drawn out into a bill. The upper temporal bar is absent, and the lower temporal bar is a slender rod called the jugal bar (the fused quadratojugal-jugal bone), which extends from the bill to the side of the streptostylic quadrate. The two vertical diapsid struts, the postorbital-jugal bar and the squamosal-quadratojugal bar, are lost. In this temporal configuration, the orbit merges with the upper and lower temporal openings. How did birds evolve this modified diapsid condition from their theropod ancestors?

In an adult oviraptorosaurian skull such as that of *Incisivosaurus* (Xu et al. 2002), both temporal fenestrae are intact and separated from the orbit by bony arches. Four bony bars frame the lower temporal opening. The vertical rostral bar is formed by the postorbital-jugal (po-j) bones, the horizontal dorsal bar by the postorbital-squamosal (po-sq) bones, the vertical caudal bar by the squamosal-quadratojugal (sq-qj) bones, and the horizontal ventral bar by the jugal-quadratojugal (j-qj) bones (fig. 15.12A, E).

The ancestral diapsid configuration is modified in early avialans birds to facilitate cranial kinesis. In the first stage of temporal modification represented by *Jeholornis*, the loss of the postorbital-squamosal bar and the considerable reduction of postorbital-jugal bar occurred. The ventral bar is transformed into a slender jugal bar, which acts as a pushrod system. The temporal configuration is further modified in *Protoavis*, where the skull has lost the rostral and partial dorsal arcades of the lower temporal opening, so that the orbit becomes confluent with the upper and lower temporal fenestrae to achieve the avidiapsid condition (Chatterjee 1997). The elimination of these blocking devices makes the jugal bar, the quadrate, and the pterygoid-palatine bar mobile to raise the upper bill (fig. 15.12B, F).

Modification of Quadrate Morphology

The avian quadrate articulates in five critical regions with the neighboring bones: ventrally with the articular, ventrolaterally with the quadratojugal, ventromedially

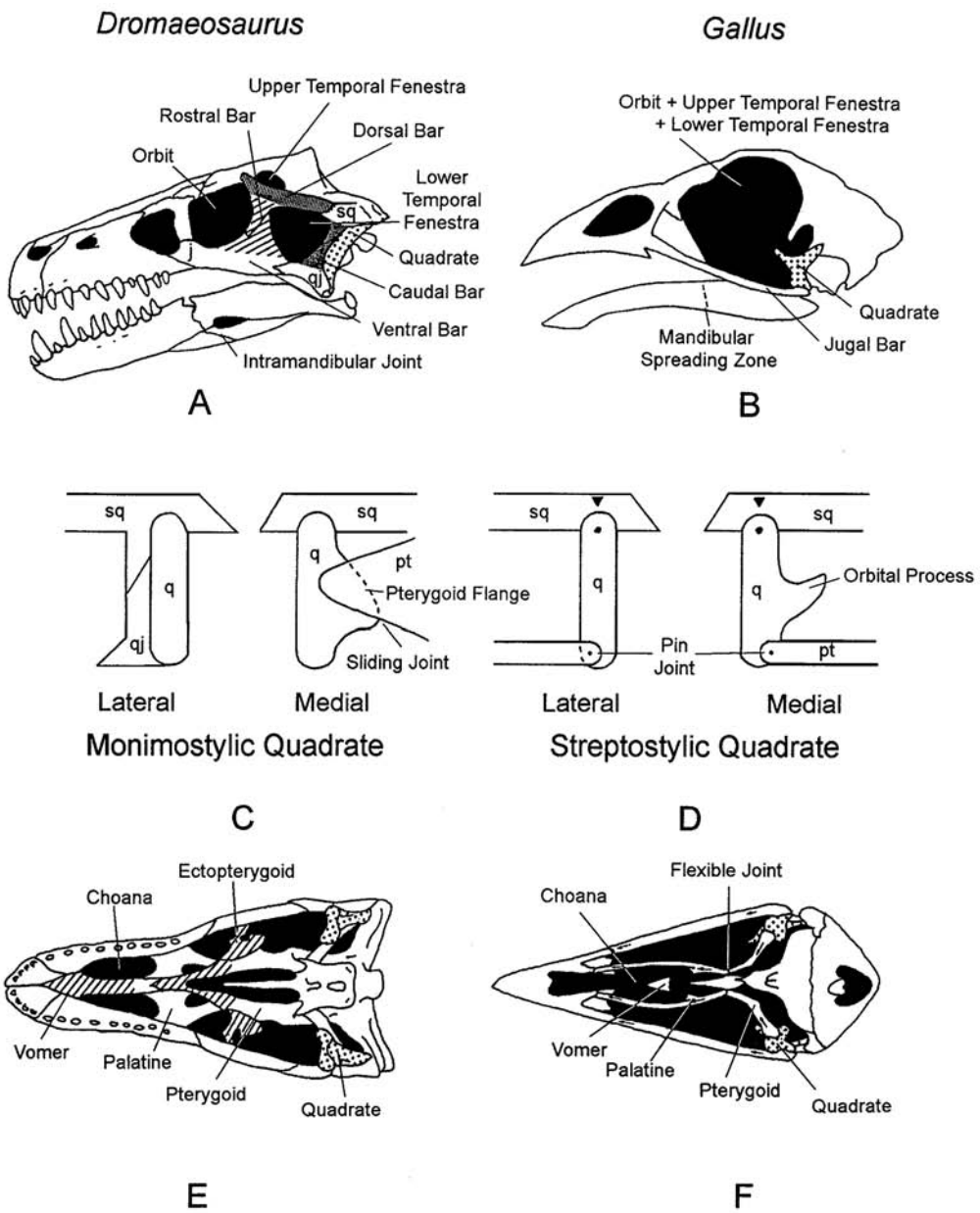


Figure 15.12. Evolution of cranial kinesis of birds from a nonavian theropod configuration, exemplified by the maniraptoran theropod *Dromaeosaurus*. A-B, lateral views of the skull showing the modification of the temporal region in response to cranial kinesis. In dromaeosaurs, the lower temporal fenestra is framed by four bony bars: the rostral, dorsal, caudal, and ventral bars. Birds acquire streptostyly and cranial kinesis by the breakdown of the rostral, dorsal, and caudal bars. The orbit becomes confluent with the upper and lower temporal fenestrae. This mechanism allows birds to raise the upper jaw. C-D, schematic diagrams showing monimostylic versus streptostylic quadrates. C, in nonavian theropods (such as dromaeosaurs), the forward movement of the quadrate is blocked by the rostral (postorbital-jugal) and caudal (squamosal-quadratojugal) bars in front of the quadrate; medially, there is a strong overlap of pterygoid on the quadrate. D, in birds, with elimination of these vertical bars and acquisition of pin joints between the quadrate-quadratojugal and the pterygoid-quadrate, the quadrate becomes mobile. E-F, modification of the palate from dromaeosaur to bird. Bony regions lost from the dromaeosaur (E) to bird (F) palate are shown by diagonally shaded areas. With the loss of the ectopterygoid, reduction of the vomer, and the development of a flexible joint between the palatine and pterygoid, the avian palate becomes kinetic. Abbreviations: pt, pterygoid; qj, quadratojugal; q, quadrate.

with the pterygoid, dorsolaterally with the squamosal, and dorsomedially with the prootic. In addition it has a free orbital process, a unique apomorphy for ornithurine birds. The avian quadrate shows great morphologic and taxonomic differences in the structure of its joint surfaces with the articular, pterygoid, quadratojugal, squamosal, and prootic bones, as well as in the shape of orbital processes. Only three aspects of quadrate morphology have hitherto been studied in detail. Lowe (1926) used the morphology of the dorsal articular head for phylogenetic purposes. Witmer (1990) studied the diversity in the number and location of quadrate pneumatopores in Mesozoic birds, whereas Chatterjee (1991) documented the evolution of the orbital process and streptostyly of the quadrate from nonavian theropods to basal birds.

In adult oviraptorosaurs, the quadrate head is firmly fixed to the adjacent bones (fig. 15.12C). It cannot move forward and backward because of a blocking device (the squamosal-quadratojugal bar). It cannot move laterally because it is sutured immovably to the quadratojugal. Medially, it receives the pterygoid near its head in the pterygoidal flange by a strong overlap. In birds, with the elimination of rostral, dorsal, and caudal bars, the quadrate becomes mobile (fig. 15.12D). The quadrate also changes its morphology and the nature of articulations with neighboring bones. It has minimized its articulations with the quadratojugal and the pterygoid and shifted their contacts ventrally to make the fulcrum more effective. Medially, the quadrate receives the pterygoid ventrally in a condyle and the quadratojugal in a cotyle to form flexible pin joints that allow streptostyly. The pterygoid flange, freed from the pterygoid articulation, forms the orbital process to create an effective lever for protraction and retraction of the upper jaw. Dorsally, it has developed a ball-and-socket joint with the braincase so that it can swing forward and backward like a pendulum.

Modification of the Palate

In maniraptorans, the palate is firmly attached to the upper jaw through the transverse strut of the ectopterygoid (fig. 15.12E). In birds, with the loss of the ectopterygoid, the palate becomes detached from the jugal and the braincase so that the thrust from the quadrate can be transmitted to the beak. In neognaths, palatal mobility is enhanced further with the development of a flexible joint between the palatine and the pterygoid. Here, the choana is displaced caudally to merge with the palatal fenestra and forms an extensive cleft down the midline. The vomer is atrophied to a sliver of bone. With these modifications, the neognathous palate becomes a delicate, elastic framework (fig. 15.12F).

Modification of the External Naris and Surrounding Bones

In oviraptorosaurs, the external naris is large, elliptical, holorhinal, positioned high and vertical in orientation, and enclosed by the premaxilla and the nasal. The nasals are fused with one another for most of their length and make extensive contact with the frontals caudally. In ornithurine birds, with the development of a long beak, the external naris has been shifted caudally. In this group, the nasal process of the premaxilla becomes enlarged and extends caudally, separating most of the nasals from the midline. The nasals become small peripheral bones bordering the antorbital fenestra and the external naris (fig. 15.12G, H). The mesethmoid is ossified and exposed between the nasals with flattening of the craniofacial hinge. This arrangement allows a prokinetic bending zone between the upper jaw and the braincase. In palaeognaths, the configuration of the external naris is controversial, and has been interpreted as holorhinal (Bock 1964) or schizorhinal (Zusi 1984). A schizorhinal naris is present in various basal neognaths such as Gruiformes, Charadriiformes, Columbiformes, and Apodiformes. In most derived neognaths, the holorhinal naris evolves secondarily from the schizorhinal naris (Bock 1964; Zusi 1984).

The Evolution of Cranial Kinesis

A survey of the temporal region, palate, and quadrate morphology of Mesozoic birds and Aves provides insight into the sequence of character acquisition during the evolution of cranial kinesis. However, this trend of acquisition of cranial kinesis appears to be mosaic in nature as different elements developed at different rates

since the Triassic and continued throughout the Mesozoic. A sequence of six adaptive stages leading to the kinetic pattern of modern birds is presented here, with each step setting the stage for the next. The discordance and concordance between the acquisition of cranial kinesis and the phylogeny of birds is attributed to heterochrony and evolutionary reversals.

Stage 1. Mandibular Spreading

Bakker (1986) suggested how theropods might have used mandibular spreading to swallow large chunks of meat when the quadrate and the intramandibular joint spread sidewise. He pointed out that the tooth-bearing dentary bones of *Ceratosaurus* were loosely bound to the tip of the snout by elastic ligaments and that a flexible intramandibular joint developed between the dentary and the posterior ramus of the lower jaw. The stationary braincase unit acted as the core of the loosely attached jaws. As the quadrate was strung outward during the closing cycle of the lower jaw, each loose joint flexed and bowed outward, just like a boa constrictor (fig. 15.13A).

A beautiful cast of the skull of a dromaeosaur *Bambiraptor* (TTU P 10364) from the Late Cretaceous Two Medicine Formation of Montana (Burnham et al. 2000) is helpful in understanding the intramandibular movement and parastyly of the quadrate. In *Bambiraptor*, as in other theropods, a loose joint occurs between the dentary and postdentary segments (Sereno 1997). The contact between the two dentaries (the dentary symphysis) is weak, with each bone having a smooth, flattened surface, which is probably indicative of a loose, filamentous attachment, allowing the dentaries to expand and bend outward. Meanwhile, the parastylic movement of the quadrate allows the spread of each quadratojugal laterally because these two bones are sutured; bending takes place at the jugal-quadratojugal scarf joint (fig. 15.13B). In nonavian theropods, the quadratojugal-jugal joint is flexible and overlapping; the quadrate-quadratojugal joint is fixed and acts as a single kinematic unit during lateral movement. Medially, the sliding joint between the quadrate and the pterygoid permits parastylic movement of the quadrate that is independent of the pterygoid. Similarly, the basal synovial joint permits some flexibility of the palate. The parastylic movement of the quadrate, in turn, pushes the articular and the rest of the caudal part of the mandible sidewise, thereby increasing the diameter of the throat to accommodate large chunks of food. Thus, the intramandibular joint is coupled with parastylic movement of the quadrate, which essentially powers intramandibular kinesis in theropods. Parastylic quadrate mobility may lead to streptostyly by loosening and reducing articulations between the quadrate-pterygoid and quadrate-quadratojugal, complemented by the loss of the descending process of the squamosal that acted as a final stop to forward motion. It thus appears that mandibular spreading is an ancient form of kinesis, a plesiomorphic feature that birds inherited from nonavian theropods.

Stage 2. Kinesis

Bock (2002) used the generic term "kinesis" to designate the beginning of avian kinesis as demonstrated by *Protoavis* with a streptostylic quadrate. Most likely, this primitive kinesis as seen in *Jeholornis* and *Cathayornis* was inherited from their maniraptoran ancestors such as *Shuvuuia* and *Caudipteryx* by paedomorphosis. Skulls of Mesozoic birds are so poorly preserved that, with the exception of the prokinetic *Hesperornis* in ornithurine birds, the exact nature of kinesis in these groups remains speculative. Moreover, the beginning of kinesis in early birds was modified by repeated heterochrony that resulted in an akinetic condition. For example, the pygostylian bird *Confuciusornis* retains the primitive pattern of intact diapsid arches, as well as primitive quadrate morphology similar to the condition of oviraptorosaurs (Hou et al. 1999; Chiappe et al. 1999). However, because of the enlargement of the eye and brain, the orbit and two temporal openings are crowded at the braincase and approach each other (fig. 15.9). As a result, the braincase becomes spherical, the lower temporal fenestra is reduced, and the toothless beak forms a rhamphotheca. The intramandibular joint, inherited from theropods, becomes a flexion zone for lateral spreading across the large mandibular fenestra. It is likely that the retention of the ancestral diapsid condition in *Confuciusornis* is a rever-

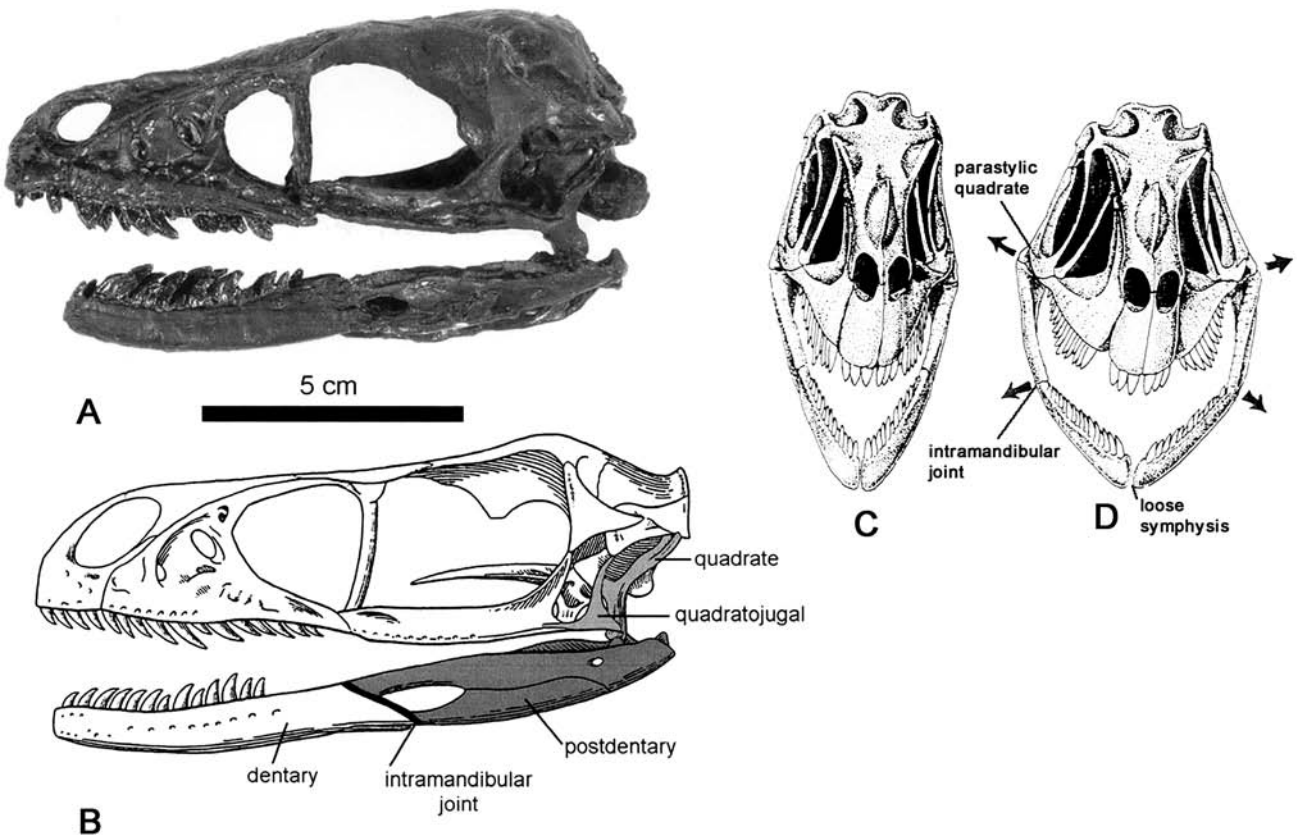


Figure 15.13. Mandibular spreading of nonavian theropods. A–B, skull and mandible of *Bambiraptor feinbergi* in the left lateral view showing the parastylic quadrate-quadratojugal kinematic unit and the intramandibular joint. C–D, front view of *Ceratosaurus* showing the coupling of the parastylic quadrate and intramandibular joint that created mandibular spreading that might assist in swallowing large chunk of meat (modified from Bakker 1986). Birds inherited mandibular spreading from nonavian theropods.

sal, a paedomorphism, not a primitive condition, which makes it difficult to trace the evolution of cranial kinesis across the phylogeny of basal birds (Chiappe et al. 1999).

The best clue of the presence of early stage of kinesis is the development of a streptostylic quadrate, which is connected to the snout by the bony palate and the jugal bar; the bony palate is unfused with the braincase with the retention of the synovial basal joint. The presence of these osteological indicators in *Jeholornis*, *Cathayornis*, and *Protoavis* indicates that these primitive birds possessed some form of avian kinesis. The first stage of temporal modification in avialans is found in *Jeholornis* with the loss of the descending process of the squamosal, the bony stop of the forward motion of the quadrate (Zhou and Zhang 2003). Here, the breakdown of the rostral arch can be seen where the postorbital lost its ventral contact with the jugal. The jugal bar becomes rod-like as it lacks a dorsal, postorbital process. The loss of the ascending process of the jugal bar may be a padaeomorphic trait. A sliding joint is developed between the lacrimal and the jugal bar. In this temporal configuration, the orbit communicates ventrally with the lower temporal fenestra. However, the upper temporal fenestra is intact with the retention of the postorbital bone. The quadrate has a primitive design similar to the condition of nonavian theropods and it lacks the orbital process. Medially it has a sliding joint with the pterygoid, which is located dorsally close to the head of the quadrate. The presence of the caudal bar indicates that the quadrate could not swing forward because of this blocking device (fig. 15.10A). However, the quadrate can move backward (opisthostyly), which, in turn, would retract the jugal bar to

depress the upper jaw from the resting position; it also would allow caudal movement of the lower jaw relative to the skull. This mechanism helps to manipulate and transport food caudally toward the throat by mandibular raking as seen in squamates (Chatterjee 1997). The enatiornithine bird *Cathayornis* retained a similar form of kinesis, possibly with additional development of a movable quadrate-quadratojugal joint (fig. 15.10C).

The second stage of temporal change is preserved in *Protoavis* (fig. 15.10D). Here, we see the beginning of the development of preorbital kinesis where the frontonasal joint allows the upper jaw to move as a unit. The orbit becomes confluent with both lower and upper temporal openings with the loss of the postorbital bone to achieve the avidiapsid condition. The vertical squamosal-quadratojugal strut at the caudal border of the lower temporal fenestra is eliminated for mobility of the quadrate. The quadrate forms a movable link between the braincase and the upper jaw via the jugal bar and the palate. It has a distinctive orbital process for muscle attachment leading to protraction and retraction of the upper jaw. Dorsally, it has a spherical head, which fits into a cup of the squamosal to form an effective ball-and-socket joint. Medially, it receives the pterygoid ventrally in a condyle and the quadratojugal in a cotyle to form flexible pin joints. Both the jugal bar and the pterygoid-palatine bar evolve into a pushrod system to transmit the force from the quadrate to the upper jaw. The ectopterygoid appears to be lost to make the palate mobile and detached from the jugal bar.

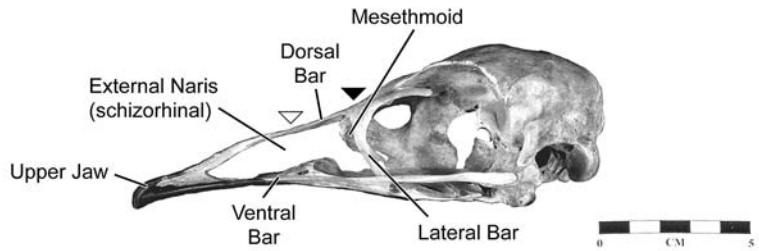
Stage 3. Prokinesis

The third stage of avian cranial kinesis can be seen in various foot-propelled, ornithurine diving birds such as *Hesperornis* and *Parahesperornis* as well as in the neornithine bird *Ichthyornis*, all from the Late Cretaceous of Kansas (Bühler et al. 1988). These Mesozoic birds developed a primitive kind of prokinesis, called here eoprokinesis to distinguish it from the highly derived neognathous prokinesis, common in modern birds. In this group, the upper jaw is rigidly constructed with a holorhinal naris and is connected to the braincase by the craniofacial hinge, which is a horizontal bony plate variously composed of thin extensions of nasal, premaxillary, and frontal bones. A flattening of the nasal-frontal hinge zone by a thin plate makes it more pliable anterior to the mesethmoid (fig. 15.14C). The quadrate head, though single, is elongated transversely to establish additional contact medially with the prootic to form a hinge joint that provides stability during streptostylic movement. It develops a pin joint with a slender jugal bar laterally and the quadrate ramus of the pterygoid medially. The temporal configuration is fully avidiapsid. The nasal process of the premaxilla becomes enlarged and extends caudally to contact the frontal, thus displacing the nasals laterally. The mesethmoid is ossified and forms a vertical pillar under the nasal. There is a gap between the nasal septum and the mesethmoid for dorsal bending. The identification of prokinesis in *Hesperornis* supports the suggestion that preorbital kinesis is primitive for postenatiornithine birds.

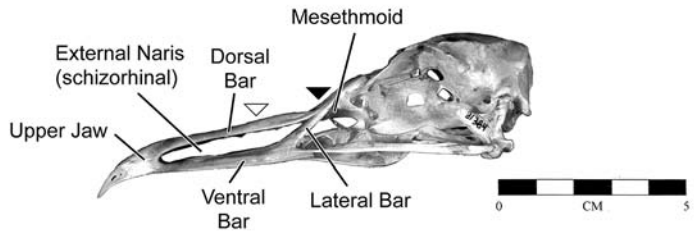
The skull architecture and kinematic units of neognaths can be derived from the ornithurine type. The skull bones of *Hesperornis* are not co-ossified, the teeth are retained, the palate is primitive with an unsegmented pterygoid, and the lacrimals travel with the upper jaw during protraction (Bühler et al. 1988). In modern neognaths, prokinesis is accompanied by the fusion of bones, a flexible pterygoid-palatine joint, loss of teeth, and the development of three types of flexion zones at the posterior end of the upper jaw instead of bony joints. Most of these features can be linked to accelerated growth by peramorphism. Moreover, the lacrimal is usually associated with the braincase segment during protraction.

Stage 4. Rhynchokinesis

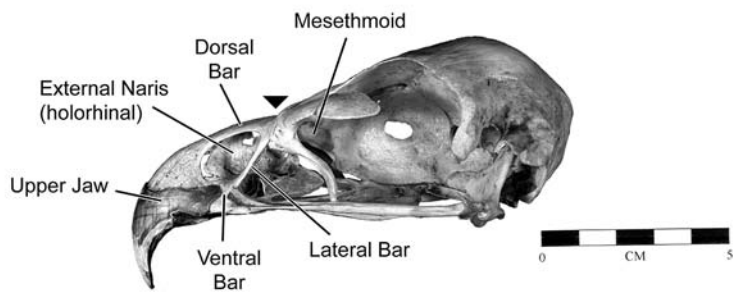
The next stage of avian kinesis is represented by palaeognathus rhynchokinesis where the ventral bar is separated from the dorsal bar by a gap, the parts of which are connected by a ligament (Bock 1964). Palaeognathous rhynchokinesis most likely evolved from primitive prokinesis, exemplified by *Hesperornis* with a holorhinal naris largely through paedomorphic retention of skull structure. The base of the upper jaw is rigid and bending takes place farther forward along the dorsal bar of the jaw



A. Paleognathous rhynchokinesis: *Dromaius novaehollandiae* (Emu)



B. Neognathous rhynchokinesis: *Larus argentatus* (Herring Gull)



C. Neognathous prokinesis: *Aquila chrysaetos* (Golden Eagle)

Figure 15.14. Three major forms of cranial kinesis among Aves, or modern birds. In each case, the upper jaw is shown in closed position in the left lateral aspect; the solid pointer indicates the craniofacial (N-F) hinge; the open pointer indicates an additional bending axis. A, palaeognathous rhynchokinesis in an emu (*Dromaius*) showing central rhynchokinesis; B, neognathous rhynchokinesis in a herring gull (*Larus*) showing proximal rhynchokinesis; C, neognathous prokinesis in a golden eagle (*Aquila*).

because of the rostral advance of the mesethmoid bone or partial ossification of the nasal septum in the region of the external naris (fig. 15.14A). A gap between the nasal septum and mesethmoid permits the rhynchokinetic hinge. The flexible lateral bar of the schizorhinal naris facilitates bending. Rhynchokinesis is possible when the ventral bar of the premaxilla and maxilla becomes thin and flexible with the loss of teeth, implying that it evolved later than the tooth-bearing prokinetic birds (Zusi 1984). The palaeognathous palate has a primitive maniraptoran design where the palatine and pterygoid are sutured; the vomer extends far back and articulates with the rostral ends of pterygoids; the elongate basipterygoid processes develop a flexible joint with the pterygoids. The first in-

dication of palaeognathous rhynchokinesis in the fossil record is documented by *Lithornis* from the Late Paleocene deposits in Montana with the development of distal rhynchokinesis (Houde 1988). *Lithornis* closely resembles tinamous in overall morphology. The latter has developed both central and extensive rhynchokinesis; central rhynchokinesis is characteristic of most ratites (Zusi 1984). Manipulation of recent skulls of ratites indicates that kinesis is extremely limited, and probably acts as a shock absorber during feeding. Gusselkoo et al. (2001) claimed that Palaeognathae secondarily lost their ability for cranial kinesis through paedomorphism.

Various forms of cranial kinesis are developed in neornithine birds, which are arranged according to their functional pathways (Bock 1964; Zusi 1984) corresponding to their phylogeny. In neognathous rhynchokinesis, the ventral bar is isolated from the dorsal bar by the external naris (Bock 1964; Zusi 1984). Rhynchokinesis is restricted to certain taxa of living neognaths (primarily some Gruiformes, most Charadriiformes, Columbiformes, and some Apodiformes). Some of these birds employ their beak tips like a probe to reach buried grubs or insects embedded in tree bark or soft substrates (fig. 15.14B). Such birds often use distal rhynchokinesis, the lifting of beak tips so that the jaws need not be parted far, to seize food. The neognathous palate is characteristic of modern flying birds. Here the basipterygoid processes are lost in adults, a flexible joint is developed between the palatine and pterygoid, by pterygoid segmentation (Balouet 1982), and the vomers are reduced. The palate forms a sliding joint with the parasphenoid rostrum, which acts as a guiding rail. Medially, the palatine-pterygoid bar effects the connection between the quadrate and the upper jaw. Among neognaths, double rhynchokinesis is common among various Gruiformes and Charadriiformes, whereas proximal rhynchokinesis occurs in three families of Gruiformes, many charadriids, the Lari and Alcae, the Columbiformes, the Trochillidae, and the Furnariidae (Zusi 1984). Most likely, neognathous rhynchokinesis evolved from neognathous prokinesis via peramorphic development of the schizorhinal nostril and an anterior shift of the flexible hinge within the nasal bone and flexible lateral bar.

Stage 5. Coupled Prokinesis

Bock (1964) recognized two kinds of prokinesis within neognaths, uncoupled and coupled; the latter presumably evolved from the former. The major morphological correlate for coupled kinesis is the presence of a postorbital ligament (or its functional equivalent, the lacrimomandibular ligament in certain ducks). Most modern prokinetic neognaths show a flexible palatine-pterygoid joint that facilitates anterior sliding of the palatal unit by the forward movement of the quadrate. Although prokinesis is present among living neognaths, the earliest form of this kinesis is documented in *Polarornis*—the Cretaceous duck from Antarctica (Chatterjee 2002), which is a contemporary of *Hesperornis*. As the quadrates are swung forward, the force is transmitted through the pterygoid bars medially to the palatines, which slide precisely on the guide rail of the parasphenoid rostrum to the premaxillae to raise the beak. The quadrate also is modified in some neognaths so that the dorsal end is bifurcated into two distinct heads for articulation with the squamosal and the prootic, respectively. The bipartite head allows considerable propalinal motion of the jaw without dislocation (fig. 15.14C). It appears that neognathous prokinesis is an ancient innovation.

Stage 6. Amphikinesis

This type of kinesis is common in Rallidae with slender jaws. The dorsal and ventral bars in this type of kinesis are flexible caudal to the symphysis, whereas the lateral bar is flexible near the craniofacial hinge. The narial opening is large and extends caudally almost to the craniofacial hinge. As a result, both prokinesis and distal rhynchokinesis are functional. Amphikinesis is probably derived from neognathous amphikinesis by gaining the craniofacial hinge of prokinesis by paedomorphism.

Phylogeny of Cranial Kinesis

Placing the diversity of cranial kinesis into a phylogenetic context may provide insights into the evolution of bill function. However, a phylogenetic perspective on avian cranial kinesis is difficult to trace because of multiple events of heterochrony and reversals that might re-

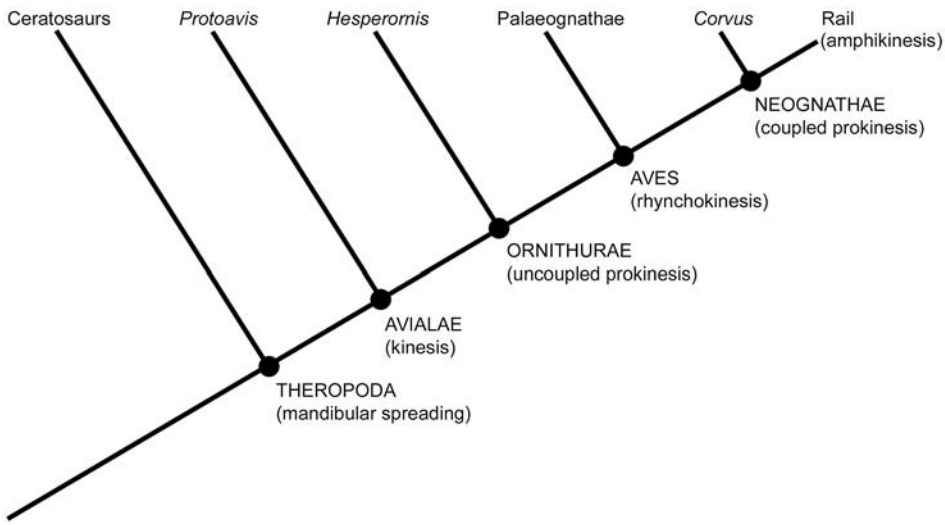


Figure 15.15. Cladogram showing the possible evolutionary stages of avian cranial kinesis beginning with the mandibular spreading of nonavian theropods with the possession of a parastylic quadrate. Avian kinesis is powered by the streptostylic quadrate. The best clue for detecting avian cranial kinesis in fossils is the partial or full avidiapsid condition of the temporal configuration with the breakdown of diapsid arches such as the squamosal-quadratojugal bar and the postorbital-jugal bar, leading to the development of the streptostylic quadrate and the development of the rod-like, slender jugal bar. The second stage of cranial kinesis is the acquisition of primitive kinesis, represented by avialans such as *Protoavis*. The third stage, uncoupled prokinesis with a craniofacial hinge, is developed in Ornithurae such as *Hesperornis* and *Ichthyornis*. The fourth stage, rhynchokinesis, is developed in Aves such as Palaeognathae. Most modern birds represent the fifth stage, coupled prokinesis. The final stage, amphikinesis, is restricted to few groups such as rails. Most likely there have been many reversal events during the evolution of avian cranial kinesis because of heterochrony.

sult from a variety of subtle and different perturbations in ontogeny. The possible evolutionary path of avian cranial kinesis is presented in a simple cladogram that shows progressive refinement of bill structure as a manipulative tool, beginning with mandibular spreading in theropod ancestors with a parastylic quadrate. Avian cranial kinesis evolved through several stages with the possession of a streptostylic quadrate, including simple kinesis in avialans and enantiornithines, prokinesis in ornithurines and neognaths, rhynchokinesis in palaeognaths, rhynchokinesis in neognaths, and amphikinesis in rallids (fig. 15.15). Both paedomorphism and peramorphism might have played significant roles in the evolution of avian cranial kinesis in different phyletic lines with reverse evolutionary changes between kinesis, prokinesis, rhynchokinesis, and amphikinesis. Cranial kinesis allows tremendous diversity in the morphology and function of the avian bills, which are not only used for feeding but also for preening, nest building, singing, courtship, and defense.

16 Birds and Humans

Hear the prayer of an earth that is stricken with pain:
In the green woods, O may the birds
Sing supreme again.

Rabindranath Tagore, *Flying Man*, 1940

Birds—the most beautiful and dynamic animals—have fascinated people for thousands of years as a universal symbol of freedom of mind and spirit. They touch our hearts with their beauty and fill our minds with wonder at their majestic flight between Heaven and Earth. They represent 225 million years of evolutionary history and epitomize the sole surviving lineage of the vanishing dinosaurs. Since the beginning of humanity, we have worshiped birds as deities, used them as symbols of power and royalty, portrayed them in art and folklore, kept them as pets, hunted them for food and feathers, and watched them for aesthetic and recreational pleasure. Thousands of years ago our ancestors immortalized birds in numerous Stone Age cave paintings in France, Spain, Africa, India, China, and elsewhere. Birds enchant us with their bright colors, striking behaviors, and melodious songs; rekindle our artistic creativity; and reconnect us with Nature. Their awesome power of flight has inspired us to conquer the air with many ingenious flying machines—airplanes, helicopters, drones, hang gliders, and rockets—but nothing we have invented so far can match the beauty, the grace, the majesty, and the complexity of a bird in flight.

During our long association with birds, however, we have also become their assailants, causing countless species to disappear. Early human colonization caused the extinction of more than one thousand bird species thousands of years ago on the Pacific islands. Bird extinctions in the tropical Pacific did not stop with these losses. Forty more species disappeared after Europeans arrived. Hunting has been a major cause of extinction, and that includes hunting for food (both birds and eggs), for feathers, and for museum specimens. In the past two centuries more than one hundred species of birds have disappeared because of human activity. Another 1,200—12% of the planet's total—face extinction this century because of our aggressive behavior, indiscriminate hunting, habitat destruction, introduction of alien predators, pesticide and pollution, international trade, and global warming. All types of birds are at risk—passerines, non-passerines, landbirds, seabirds, big birds, and small birds.

There have been five great extinctions in the history of Earth, the last one of which killed off the dinosaurs. Many scientists think a sixth is underway. Conservationists

warn that many birds face the same fate as their dinosaur ancestors. However, this time the killer is neither asteroids nor a volcano that is threatening to finish them off. The culprit, they say, is the "wise man," or *Homo sapiens*—and therein lies the great tragedy. When he paddled across the Pacific, he exterminated 50% to 90% of the bird life on islands he colonized. As his technology improved, so did his destructive power. When he cleared the rainforest, many birds lost their habitats. If there is any hope of reversing the trend, it lies in increasing public interest, awareness, and action in conserving our feathered friends. Since the environmental movement took off in the 1960s, the importance of preserving biodiversity is becoming more widely understood.

The Quaternary Extinction of Birds: Human Impact

Birds endured a major mass extinction at the end of the Cretaceous, but they rebounded from this crisis and explosively radiated during the Tertiary period. Since then, the number and variety of species has progressively increased to the present peak of diversity. However, birds are now at risk because of the effects of human activity. People are directly responsible for the extinction of many wild birds. Some species have been hunted to oblivion. Others have been killed off as people destroyed natural habitats to make room for their own settlements. Human beings have also polluted the environment, which has wreaked havoc on bird diversity. These assaults started a long time ago when early humans began migrating to new frontiers and confronting pristine habitats. Extinctions of birds were more severe on islands than on continents. Edward O. Wilson (1992), the famous American naturalist, named these human-induced catastrophes "centinelan extinctions" after the Ecuadorian ridge Centinela in the Andean foothills of Ecuador. Centinela witnessed the collapse of biodiversity and wept silently because of human interference. Today, humans seem to be creating a sixth major mass extinction event.

Extinction of Island Birds

The remote islands of the eastern Pacific were the last habitable regions on Earth to be colonized by humans from 700 to 3,500 years ago. Before human colonization, many islands, such as Samoa, Tonga, Hawaii, New Zealand, Madagascar, and Mascarene, supported a rich and varied endemic biota. The tropical climate and abundant rainfall gave rise to dense rainforests. Because of isolation and lack of predation, many birds on these islands became secondarily flightless. They evolved without mammalian predators and thus had little defense against humans, and their rats, dogs, cats, and pigs. Biotic crises began thousands of years ago when early human explorers began to colonize these islands and exploit their resources. Among landbirds, megapodes, rails, pigeons, parrots, kingfishers, and passerines were the major casualties. The early Polynesian settlers hunted the easy prey, destroyed natural habitats, and pushed many avian species to the brink of extinction. Bird populations were reduced further with the clearing of forests and introduction of mammalian predators that preyed on eggs, nestlings, and adult birds. The impact of alien species is most catastrophic in a restricted area, notably a small island, which offers very limited opportunities for retreat. From archaeological sites, sinkholes, lava tubes, sand dunes, and flooded caverns, Storrs Olson, Helen James, David Steadman, and Richard Duncan have pieced together the telltale evidence of human-caused avicides on these Pacific islands. The statistics of destruction are staggering: about 2,000 species of birds have been extinguished in the past 3,500 years, principally following the human occupation of these islands (Olson and James 1984, 1991; Steadman 1995, 2006; Duncan et al. 2013). Bird species that were flightless and large-bodied had a higher rate of extinction because they were easier and more profitable to hunt than those that could fly. Disappearances are linked to overhunting by people, forest clearance, and introduced species. Though human impacts were widespread and rapid in the Pacific islands within a few hundred years of colonization, geographical features as-

sociated with island size and rainfall mediated the extinction pattern of avifauna.

The Hawaiian Islands (fig. 16.1) stretch in a great arc, some 2,500 kilometers long, in the North Pacific Ocean, about midway between California and Japan. The first settlers in Hawaii were Polynesians. They reached these remote Pacific islands about 1,500 years ago by means of rafts and dugout canoes from western archipelagoes of Melanesia and Micronesia. They cut and burned the forests to plant taro and other crops and brought dogs, pigs, and rats into the virgin ecosystem. They encountered only two species of mammals—a bat and a seal—but abundant bird life. They ate fish, turtles, and a wide variety of flightless birds, which, being slow-footed, were easy to catch. Among the first to be extinguished were some geese, such as *Thambetochen*; the tortoise-jawed moa nalo (*Chelychelynechen*); several varieties of rails (*Porzana*), ibises (*Apteribis*), owls (*Grallistrix*), and finches; an eagle (*Haliaeetus*); a hawk; and a petrel. Clearing of forests by early settlers must have contributed heavily to the destruction of many species of passerine birds. The exotic predators that harmed endemic species through predation, competition, and disease may have precipitated other crises. It is estimated that about sixty endemic species were lost because of the interference of Polynesian colonists.

A second wave of extinctions followed the arrival of Europeans in the eighteenth century, with more forest clearing and more introduced mammals, such as cattle and goats. Most of the natural habitat was lost to cultivation, browsing, and fire, eliminating another twenty to twenty-five species. Among the victims were an eagle, a flightless ibis, a strange owl, honeyeaters, honeycreepers, finches, and a dozen other landbirds.

The human-induced extinctions on Hawaii were truly enormous, extinguishing 70% of the species that had made up the total avifauna. Centinelan extinctions on the same grand scale also occurred on other Polynesian islands, such as Henderson, Marquesas, Society, Cooks, Samoa, Tonga, and Polynesian outliers of Melanesia. Today, the avian fauna on Hawaii and other Pacific islands is highly impoverished because of human influence.

Another arena of destruction is New Zealand, the southwestern outpost of the Polynesian migrations. Lying about 1,600 kilometers southeast of Australia, it has been separated from other Gondwana continents since the Cretaceous and lacked native mammals (except for bats) before human settlement. In this splendid isolation, giant flightless birds like moas thrived, especially in the South Island temperate forest. The first people to live in New Zealand were the Maoris, a Polynesian tribe that arrived about AD 900. Maoris lived mainly by fishing and hunting moas. When Maoris settled in New Zealand, they encountered fifteen species of moas ranging in size from that of large turkeys to giants weighing more than 250 kilograms. The moas were grazing animals and were defenseless. The Maoris aggressively hunted moas in large numbers and robbed their nests. Hundreds of archaeological sites testify to the indiscriminate slaughtering of moas all over the islands, with bones and eggs preserved in ancient kitchen middens. It took the Maoris about six hundred years to hunt the moas to extinction. They also wiped out twenty other landbirds, including nine additional flightless species. Humans had a devastating effect on the biota of New Zealand, which has lost forty-four endemic species of landbirds during the past millennium.

Centinelan extinctions were also rampant on the islands of the Indian Ocean (fig. 16.2). Madagascar is the fourth largest island in the world. A rift separated it from Africa and India during the Cretaceous, and it moved southward and then, over millions of years of isolation, evolved an exotic biota that included several species of majestic elephant birds. These robust ratites were important grazers and browsers in the tropical forest, and the largest species attained heights of more than 3 meters. They resembled heavyweight ostriches with massive legs and weighed about 450 kilograms. Immigrants from Indonesia moved to this island in successive waves between 1,500 and 2,000 years ago, followed by African settlers. It is likely that these Malagasy settlers hunted not only the elephant birds but also their huge eggs. The eggs, about 34 centimeters long and 11 liters in capacity, were used

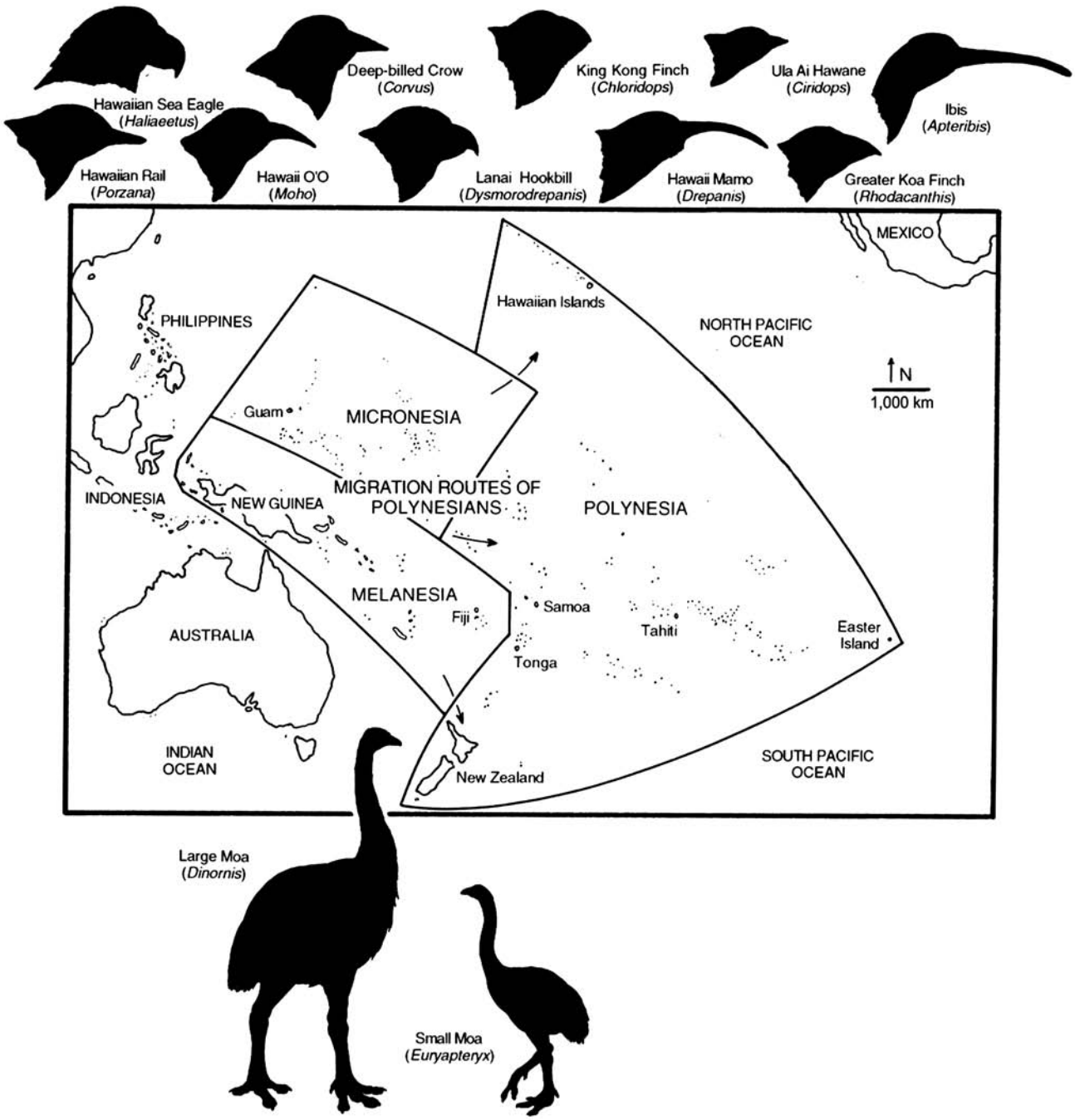


Figure 16.1. Human-induced extinctions of flightless birds in the Pacific islands; *top*, silhouettes of bird victims in Hawaii (Royte 1995); *center*, map of various Pacific islands colonized by the Polynesians; *bottom*, silhouettes of the giant and small moas of New Zealand.

for both food and containers. The beaches of Madagascar are still littered with eggshells of elephant birds. These defenseless birds became easy prey for the arriving humans. Larger animals generally had smaller populations and lower reproductive rates, making them vulnerable to overexploitation. Continued hunting and egg collecting over centuries, along with habitat destruction, led to the extinction of the largest birds that ever lived. The last living elephant bird, *Aepyornis*, was reported in 1658.

A similar sad story of avian extinction was repeated in

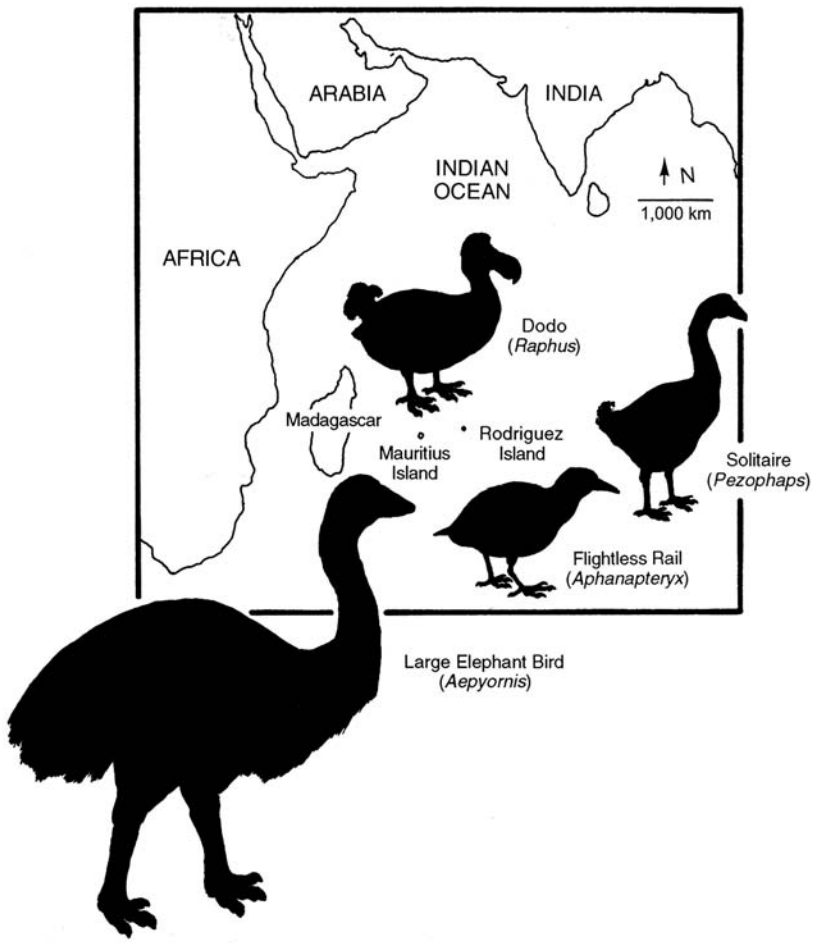


Figure 16.2. Human-induced extinctions of flightless birds in the islands of the Indian Ocean: the recently extinct dodo of Mauritius, the solitaire and flightless rail of Rodriguez Island, and the large elephant bird of Madagascar.

the Mascarene Islands with the arrival of Europeans during the fifteenth century. The Mascarene Islands lie east of Madagascar and constitute several landmasses formed by the Deccan hotspot trails, including Réunion, Mauritius, and Rodriguez, which were isolated for millions of years during the northward drift of India. The total number of human-induced bird extinctions in the Mascarenes is close to thirty species, including several species of rails, waterfowl, and landbirds. The most famous casualties are the dodo (*Raphus*) of Mauritius and the solitaire (*Pezophaps*) of Réunion and Rodriguez Islands. These large, flightless pigeons had great body size (approximately 20 kilograms) and substantially reduced pectoral limbs. They were well adapted to these islands and evolved into many strange and colorful species before the arrival of their formidable enemy. European sailors hunted the dodos and solitaires for sport and provisions mercilessly. The newly introduced monkeys and pigs relished their eggs. Their extinction was so rapid and so complete that the vague descriptions given of them by early navigators were long regarded as mythical. By 1680, dodos were gone forever. The extinction of solitaires probably happened a century later.

In the pattern of extinction among island birds, large flightless birds were the main victims because of overkill. These birds, having never before seen human beings, were unafraid of people and were easily approached and killed. Flightless rails were also severely threatened on these islands. Many of the extinct species come from six groups: ratites, rails, waterfowl, pigeons, crows, and

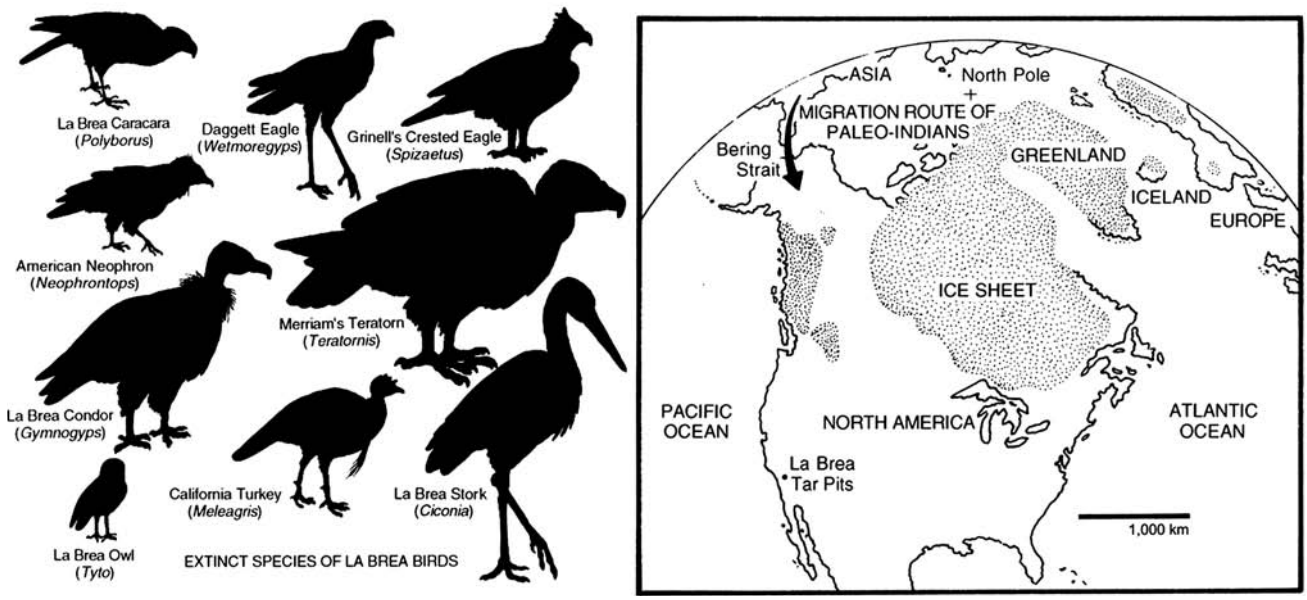


Figure 16.3. *Left*, silhouettes of various extinct species from the La Brea tar pits; *right*, paleogeography of North America during the last ice age. The Paleo-Indians arrived about 12,000 years ago; note the location of La Brea tar pits in Los Angeles (Harris and Jefferson 1985).

birds of prey. The clearing and destruction of forests for agriculture fragmented the habitat of native species, contracted their range, reduced their resources, and caused their populations to dwindle. There was nowhere left to feed, hide, or escape. The surviving island birds are, for the most part, mere relics of a rich avifauna that vanished not long ago.

Extinction on Continents

On most continents where humans and birds evolved together for millions of years, the effect of humans on the diversity of birds was minimal—until recently. In North America, the major extinction of birds coincides with the arrival of Paleo-Indians 12,000 years ago, by way of the Bering land bridge. These Paleo-Indians were such successful big-game hunters that their populations expanded and spread rapidly—perhaps by about 16 kilometers per year. By 10,000 years ago, humans occupied most parts of both North and South America. During this time most of the large mammals—mastodons, saber-tooth cats, camels, giant beavers, and lemurs—became extinct as did many species of birds that had fed on them (fig. 16.3). Whether early Indians armed with sophisticated stone tools and projectiles destroyed the mammalian megafauna remains controversial. There has been a continuing debate over whether human hunting or climatic change was to blame for the extinction of large mammals in the Americas. The close chronological coincidence between the extinctions of large mammals and the arrival of big-game hunters in North America is striking, however.

If, within a few thousand years of their arrival, the Paleo-Indians threatened the populations of large mammals of North America by overkill or blitzkrieg, as maintained by Paul Martin (1984), then human interference had indirect repercussions on the elimination of the Late Pleistocene avifauna. This avian crisis is very unusual because, of nineteen extinct species, most were large predatory birds—teratorns, condors, vultures, carrion storks, hawks, and eagles—that scavenged on large mammals. None of the birds was suitable for human predation for food. However, the extinction of large mammals surely had a ripple effect on the scavengers that fed on them.

The short supply and eventual lack of large carrion disrupted the food chain. In most cases the avian extinctions in North America cannot be attributed directly to human interference, except for a flamingo and one anatid, *Chendytes* (Steadman and Martin 1984). In recent times, the passenger pigeon, Carolina parakeet, Labrador duck, great auk, and heath hen have become victims of humanity. However, there is a troubling forecast. A recent Audubon report predicts that 314 North American bird species will be at risk from climate change by the end of the century (Nijhuis 2014).

The Recent Crisis

The effects of humans on avian diversity and that of other biota have become increasingly disastrous. Since the time of Christ, 20% of the bird species worldwide have become extinct, 11% of the surviving species are seriously endangered, and more than 50% of the world's birds are declining in numbers (Wilson 1992). Specialized, large-sized, and rare species, and those with restricted ranges, are especially vulnerable to extinction. The wild-bird trade is a growing threat to survival of some species. Parrots are the most popular of all cage-birds, and the trade in some species has had devastating effects. The parrot family is the most threatened group, with more than seventy species at risk. This is an alarming signal. Recent statistics are not encouraging. Since 1860, approximately eighty species of birds have been lost. Overkilling, habitat destruction, and the introduction of exotic species have contributed to the past demise of avian species. In recent times, pollution, pesticides, nuclear waste, and human overpopulation have compounded the crisis. The most alarming human assault on the environment is the contamination of air, earth, rivers, and seas with dangerous pollutants.

We are stealing from future generations the basic necessities of life. We are not only polluting the environment, but also increasing our territory and range. It has been estimated that the human population will exceed 8 billion sometime in the next fifty years, making ever greater demands on Earth's resources. As human populations expand, the demand for resources will continue to threaten those remaining habitats and the living things within them. As our culture and technology overtake the planet, other living things have less room and are pushed to extinction. In our thirst for water, our hunger for land, and our appetite for natural resources, we have altered large areas of habitat for human settlement. Many species in shrinking habitats will find it increasingly difficult to live in a world dominated by *Homo sapiens*, the most universally predatory species that has ever existed. With our technology and explosive growth, we are rapidly threatening many other species, ones that have been around millions of years longer than us.

It seems that our planet will increasingly become the home of a single aggressive species. This will have a cascade effect on the destruction of habitat and biodiversity. We are now victims of our own success and have not adequately assessed the dark side of our achievement. The pumping of greenhouse gases into the atmosphere and the depletion of stratospheric ozone have serious consequences for the global climate and ecology. The ice caps from the polar regions are melting at an alarming rate, causing a rise of the sea level and the drowning of some lowland habitats. Will the rainforests survive? Will there be any wilderness left for wildlife? Will the lakes and the rivers be contaminated with pesticides and pollutants, killing all their inhabitants? Will desertification claim more and more arable land? Will Nature take her revenge with recurrent crop failures, volcanic eruptions, earthquakes, floods, droughts, diseases, and pestilence to bring us in line with the rest of life? Are we precipitating another biotic catastrophe, the sixth great mass extinction? Many believe so. This time the agent of destruction will not be a bolide from outer space, but homegrown human beings. It is not clear whether the survivors will include our species after the recovery.

Another threat for the collapse of avifauna in islands is the introduction of exotic species—predators such as feral cats and rats; herbivores such as goats and pigs, which degrade native habitat; diseases such as avian malaria and pox transmitted by non-native mosquitoes; and plants

that displace native species and reduce habitat quality for native birds. Pollution remains a threat to about 9% of globally threatened bird species, mainly by causing either elevated mortality or reduced reproductive success. Fertilizers and pesticides used in agricultural areas adjacent to tropical forests can take a toll on forest avifauna, especially among raptors, when they feed on contaminated mice and rats.

The American marine biologist Rachel Carson in her influential book *Silent Spring* (1962) turned our attention to conservation of birds, especially environmental problems she believed were caused by synthetic pesticides such as DDT. DDT was implicated in the dramatic declines in the breeding populations because of the production of thin-shelled eggs, which could break under the weight of an incubating parent. Reproductive failure in some birds, particularly the brown pelican, osprey, eagle, and peregrine falcon, eventually resulted in epic population declines in the United States that led to a nationwide ban on DDT in 1972. Since its ban in North America, populations of many raptors have recovered, but DDT is still being used in many developing countries for malaria control. *Silent Spring* was a clarion call in the wilderness that inspired a grassroots environmental movement and led to the creation of the U.S. Environmental Protection Agency in 1970. To strengthen the conservation movement, Congress passed the Endangered Species Act in 1973 and the Wild Bird Conservation Act in 1992, recognizing that our rich natural heritage is of "esthetic, ecological, educational, recreational, and scientific value to our Nation and its people." Under these acts, a species may be listed as either endangered or threatened. "Endangered" means a species is in danger of extinction throughout all or a significant portion of its range. "Threatened" means a species is likely to become endangered within the foreseeable future. However, these conservation laws are not universal. The majority of threatened birds live in developing countries where funding for conservation takes second place to the needs of people. The use of pesticides and pollution of the environment threaten many migratory bird species throughout the world today. The species of birds at risk of extinction and those that are potentially threatened or declining must be saved with international cooperation and funding. Yet it is not all gloom and doom. There have been a few species that have rebounded once we helped them.

Conservation

Against this gloomy background we must decide the future of biodiversity and the fate of avifauna. Birds pollinate flowers, disperse seeds, scavenge carrion, deposit nutrients, control pests, and provide food, acting as essential drivers of ecosystems. Our actions are now causing many of their populations to decline. It is our responsibility to reverse this trend. The world's rare birds need our help if they are to survive. Birds are sensitive indicators for detecting environmental disturbance—they are closely linked to all other wildlife on the planet, and problems for birds serve as warning signals for the survival of plants, other animals, and people. As Wilson (1992) asserted, we have to develop an environmental ethic for long-range plans to save this fragile planet. The conservation of biodiversity is a global responsibility. Wildlife does not recognize political boundaries. Each county, each state, each nation, and each international agency has a necessary role to play in finding new ways to manage biological resources.

The widespread interest in birds and conservation initiatives has likely prevented two-thirds of bird extinctions in the past thirty years. Bird conservation practices are increasingly necessary to address the impacts of human activities that have accelerated extinctions and continue to threaten bird populations worldwide. There are several threats for the decline of bird population worldwide because of human impacts: habitat loss, development, mining and drilling, agriculture, grazing, invasive species, diseases, communication towers, wing turbines, power lines, hunting, pollution, pesticides, acid rain, marine trash, and climate change. Invasive species are responsible for the extinction of many bird populations. In recent times efforts have been made to combat such species. We can eliminate some of the threats by direct

interventions, public pressure, and regulatory change, we can conserve habitats, and we can halt extinctions of endangered species.

The tropical region is at the forefront of bird extinction and endangerment because of deforestation. Habitat fragmentation and habitat destruction are the largest single threat to biodiversity. The direct causes of deforestation are numerous, including spread of agriculture, logging, mining, and urbanization that threaten more than a thousand species of birds (87% of all threatened species). Tropical forests are disappearing at a rapid rate while the remnants face an increasing number of threats for the survival of birds. With the disappearance of forests, sedentary birds are more extinction-prone than are mobile species. Other habitat types in the tropics such as mangroves, swamp forests, dry forests, and savannas face similar predicaments. As available habitat shrinks by 50%, the number of species declines by 15%. Habitat protection is therefore one of the most frequently used conservation interventions, particularly in the tropics and in other areas with large areas of surviving natural vegetation. The Nature Conservancy has done an admirable job in preserving plants and natural communities that represent the diversity of life by protecting the land and waters they need to survive. Protected areas (parks and reserves) cover about 12% of Earth's land surface. Maintaining, and even expanding, existing protected areas is critical for the survival of sensitive tropical bird species. However, funding is lacking even to maintain protected areas in tropics. Many of these preserves are small, and we must take additional steps to conserve biodiversity before we are overtaken by another catastrophe. Migratory birds in the tropics are especially vulnerable because they spend the nonbreeding season in the tropics, but breed and winter in different geographical regions when they are exposed to pollutants and pathogens that can cause population declines. Another threat to migratory birds is large-scale hunting and trapping for food.

The most useful technology for conservation is remote sensing, now widely used for monitoring deforestation and species distribution. Remote sensing, combined with economic progress, has helped many countries to reduce deforestation and encourage conservation. Other than habitat protection, scientists and conservation professionals have developed a number of techniques of varying levels of success to protect bird species. These conservation measures include captive breeding of endangered species to save species from extinction, reintroduction of captive-bred populations into the wild, and translocations of threatened species into areas of suitable habitats currently unused by the species.

Conservation happens at local, national, and global levels. Concern over declining waterfowl populations has fueled efforts for wetland conservation since the 1930s. Similarly, increased regulation and prohibition of certain pesticides reversed declines in raptor populations. Many migratory birds are disappearing from our forests and meadows at alarming rates. As they migrate back and forth from continent to continent, they can no longer find safe places to stop for food and rest. We can take several measures individually and collectively to save threatened species from extinction. It is the right thing to do, both morally and ethically, as the dominant species on the planet, so that we can pass on to future generation the wonder worlds of birds that existed when we ourselves arrived on the planet. Along with conservation, we must educate the public about the potential dangers created by ourselves. We have to clean up some of the mess that we have made of our surroundings. We have to raise awareness of our endangered species among the general public through campaigns and information at national and international levels. These are perilous times for life on Earth. It is in our own best interest to safeguard the birds and biosphere and avert the sixth extinction. When we save biodiversity, we are actually saving ourselves. This is the only home in the entire Solar System that we can share together.

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